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Perrissodactyla

Perissodactyls are the odd-toed, herbivorous ungulates. The extremities, at least behind have 3 or 1 digits, the weight of the body resting exclusively in a line with the 3rd digit, thru which the mesaxon goes, dividing it into symmetrical halves.

The heel has only one proximal articular surface. The calcaneum does not articulate with the fibula. The femur has a 3rd trochanter. 23-22 thoracic-lumbar vertebrae. Nasals broad posteriorly. Alisphenoid canal present. Tympanum small, ring-formed or only a little inflated. The cheek teeth form a closed row and are either lophodont or selenolophodont. Premolars molariform, except in Eocene forms.

The stomach is simple, the coecum large and broad. Gall bladder absent. Testicle inguinal, sometimes scrotal. All accessory sex glands present.

Geographic distribution.

The recent Perrissodactyls, with the exception of some groups of horses, are confined to the tropics and subtropics.

Present in Central, Southern, and Western Asia, Africa, India, Sumatra, Borneo, Mexico, South America.

The earliest perrissodactyls found are of the Wasatch stage of the Lower Eocene of Europe and North America. No probable ancestors of the group are present in the Paleocene of either continent.

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Family 1. Tapiridae

Dental formula

$\frac{3}{3-2}, \frac{1}{1}, \frac{4-3}{4-3}, \frac{3}{3}$, Premolars more often lost in lower than in upper jaw. Lophiodon only one with but 3 P

Incisors chisel-shaped, canine conical, and moderately large. Diastema between canine and premolars. Back teeth brachyodont, with cingulum and parastyle. Primitive cusps remain distinguishable -- bunolophodont. No cement. Premolars increasingly like molars thru evolution of group. Upper molars: paracone and metacone connected together in the ectoloph; two transverse ridges connect these with the inner cusps; strong parastyle. Lower molars: bilopholophodont; two right-angled transverse ridges directed oblique to the long axis.

Skull long. Nasals originally long, becoming, later, short and freely projecting.

Orbit and temporal fossa not distinct.

Ulna and fibula complete.

Manus, 4 digits; pes 3 digits.

Extremities are longer and more slender than most Rhinoceriotids, but heavier than most Equidae.

In the carpus, the scaphoid articulates on the trapezoid and the magnum, and the lunar (on the larger part) on the unciform. The magnum carries the greates weight and is supported by metacarpals II and III.

The femur has a well developed third trochanter.

The astragalus possesses a deep trochlea, and distally a large flat articulation for the navicular and a smaller one for the cuboid.

The tapirs (genus Tapirus) are the only members of the family Tapiridae which are not extinct. Modern tapirs live in southern Asia and Tropical America. Members of this family originated in the lower Eocene of Europe and North America. They remain in Europe until the Pliocene, and in China and North America in the Pleistocene.

The nearest relatives of the Tapiridae are the Rhinocerotidae.

Subfamily 1. Lophiodontinae

Dental formula

$\frac{3}{3}, \frac{1}{1}, \frac{4-3}{4-3}, \frac{3}{3}$.

Upper and lower molars with two oblique transverse ridges. Paracone of upper molars lengthened. Metacone of upper molars concave. All premolars, even the foremost, molariform. Teeth lophiodont.

Manus 4, pes 3 digits.

Geologic range: Abundant and varied thruout the Eocene of Europe. Not prominent in North America, but extending from Lower Eocene thru White River Oligocene of North America (one stage later than in Europe).

Genus Heptodon Cope.

Dental formula

$$\frac{3}{3}, \frac{1}{1}, \frac{4}{4-5}, \frac{3}{3},$$

All premolars the same as molars. M$_{4-5}$, 3-ridged.

Found in the Lower Eocene deposits of Wyoming, Wasatch and Wind River.

Genus Helaletes Marsh (Hyrachyus, Lophiodon, Desmatotherium Scott.)

Dental formula

$$\frac{3}{3} \frac{1}{1} \frac{4}{3} \frac{3}{3}$$

Double internal cusp on premolars. Long diastemata before and behind upper canine.

Helaletes is the smallest known representative of the tapiroids. Its relationship with the tapir is indicated, according to Troxell (1922) by the following important characteristics:

Position of the antorbital foramen

Rising of the sagittal crest

Trend toward molariformity in the premolars

Low maxillaries

Pit in front of the orbit, which may have given rise to the receded nasal aperture of the modern tapir.

It seems impossible to derive Helaletes from the larger Heptodon which precedes it, tho this has been suggested by some authorities.

Geologic range: Present in the Bridger beds of Middle Eocene and the Uinta beds of Upper Eocene.

Figures of Helaletes may be found in Troxell's "Helaletes Redefined" (1922) and in Zittel (

Genus Lophiodon Cuv. (Tapirotherium Blv.)

Dental formula

$$\frac{3}{3} \frac{1}{1} \frac{3}{3} \frac{3}{3}$$

The largest of the tapiroids are found in this genus. They are regarded as a stock which died out without giveing rise to later forms.

Lowerm molars with straight ridges. Lower molar 3 with third lobe.

The second transverse ridge of premolar 3 above is usually incomplete.

Skull low, and long, with a high crown. Occiput overhanging. Nasal bones reaching to a point above incisor 1.

Thruout the eocene, the Lophiodons varied in size between that of a pig, (L. Occitanicum) and that of a Rhinocerus, (L. rhinocerodes). Lophiodon is present in the Sparnacian and Ypresian deposits of Europe (Eocene) and the White River deposits of North America (Oligocene).

Colodon Marsh

This genus combines the characters of horses and tapirs, but as Scott points out it is by no means a connecting link between the two families.

Teeth tapir-like, expecially in the lower jaw. Premolars molariform.

Limbs light and slender

Feet long and narrow -- forefoot retaining small 5th digit.

Hind foot, in particular, resembles contemporary horses (Mesohippus), tho the median digit was not so enlarged or the lateral ones so greatly reduced.

Geologic range: White River Oligocene. Died out in Oligocene.

Subfamily 2. Tapirinae

Dental formula

$\frac{3}{3}, \frac{1}{1}, \frac{4}{4-3}, \frac{3}{3},$

Premolars increasingly molariform. Upper molars with conical paracone and metacone of the same length. Lower molars with transverse ridges. Molar 3 below with or without Hypoconulid.

Geologic range: Eocene to Pleistocene in North America; Oligocene to Pliocene in Europe; first appear in the Pleistocene in Asia and South America, and are living there today.

Genus Systemodon Cope.

Most ancient of the tapirs. No larger than a coyote. No proboscis and not resembling a tapir outwardly. (Scott)

Premolar 4 in both jaws near the canine. (no diastema). Outer cusps of the upper molars almost equally strong. Ridges with distinct intermediate connecting cusps. Premolar 1 above small, and having a single cusp. The remainder of the premolars are 3-cusped. Molar 3 has 3 lobes.

Geologic range: Lower Eocene Wasatch of Wyoming and New Mexico.

Genus Protapirus Filhol

Premolar 4 above with 2 outer cusps and a 2-pointed inner cusp. Molar 3 below 2-lobed. In the American spedies of Protapirus, the lower molars stand as 2 almost isolated protruberances.

Protapirus is much smaller than the Pleistocene or the recent tapirs (about one-half the size). The teeth indicate the origin of the tusks from the canines, both above and below. The upper incisor evidently replaces the upper canine at a later date.

The pattern of the grinding teeth is identical with that of the modern genus, but the premolars were not as yet all molariform.

The development of the proboscis already begun. Nasal bones show beginning of shortening. Little else known of the skull.

Bones smaller and lighter than in the modern tapirs.

Geologic range: Lower Oligocene White River of North America and Mid. Oligo. of Europe. First occurrence in Europe in the Stampian. Upper Oligocene John Day.

Tapiravus Marsh

Browsing tapir of the Upper Miocene of New Jersey (Hipparion zone) and Lower Pliocene of the Rocky Mts.

Genus Tapirus Linne (Elasmognathus Gill)

Upper premolars with the exception of premolar 1, molariform, but oblong, and with weak parastyle. Premolar 2 elongated. Skull with very short, anteriorly shapr-pointed nasals, sometimes supported by a partition.

Teeth low crowned. Pattern of teeth simple. Two elevated, straight transverse crests on both upper and lower grinders.

Upper incisors and lower canines form tusks (externally enlarged) Upper canine greatly reduced and functionless.

Genus Tapirus Linné

Dental formula

$$\frac{3}{3}\ \frac{1}{1}\ \frac{4}{3}\ \frac{3}{3}$$

First and second incisors above nearly equal, having short broad crowns. Third upper incisor, large and conical, larger, in fact, than the canine, which is separated from the incisors by a short diastema.

The lower incisors diminish in size from the first to the third. Canine is large and conical, forming the tusk of the lower jaw. It works behind and against the third upper incisor.

A diastema is present between the canine and the cheek teeth in both jaws.

The premolars, with the exception of $P\frac{1}{}$ and $P\frac{2}{}$ are the same as the molars, having four roots in the upper jaw and quadrate crowns, wider transversely than longitudinally, with four cusps connected by a pair of transverse ridges (one anterior, one posterior). In the lower jaw the molariform teeth are composed of a simple pair of transverse crests with a small anterior and posterior cingulum. $P\frac{1}{}$ lacks the anterior inner cusp and thus has a triangular crown. $P\frac{2}{}$ is narrow anteriorly and has an anterior third lobe.

Skull elevated and compressed. Orbit and temporal fossa widely continuous. No postorbital process of the frontal. Anterior nasal aperture large, extending well up on the face between the orbits. Nasal bones short, elevated, triangular, and pointed in front.

Limbs short and stout.

The first digit of the manus is absent. The other 4 bear hoofs. The third is longest, the second and fourth nearly equal, the fifth very short and scarcely reaching the ground when standing.

3 toes of pes typically Perissodactyle in arrangement; 3rd toe largest, the second and fourth nearly equal.

Geologic range: Upper Miocene and Pliocene of Europe; Pliocene in the Upper Siwaliks; Pleistocene of China (Scott includes it in the Pliocene of China) Pleistocene and Recent in South and Central America; Pleistocene in North America. Living in South and Central America and Southern India.

General account of tapirs from Scott (1913).

At the beginning of their history the tapirs were small, and tho growing larger thru their evolution, have never become large.

The most distinguishing feature of the living tapirs is the long proboscis, a flexible, dependent snout. The skull is modified accordingly, the nasals being shortened. The tapir has small tusks, which, however, do not show when the mouth is closed (Incisor $\frac{2}{}$ and lower canine)

The limbs are short, and moderately heavy, the bones of the forearm and lower leg are separate.

Body covered with smooth, short hair, which in the American species, is a uniform dark brown. In the Asiatic species the neck and limbs are black, the body white. The young have longitudinal, light-colored stripes which Scott considers indicative of the ancestral color of the adults.

Tapirs are borwsing animals, as indicated by the low-crowned teeth. They are shy and solitary, and live in thick forests near the water, frequently entering the water for bathing or as a place of refuge when pursued.

Tapirs are the only modern representatives of the perissodactyles in the western hemisphere.

Family 2. Rhinoceridae

The skull is low and elongated. A sharp occipital ridge is present. The orbits are open behind. The temporal fossa is very large. The nasals project freely, and among the modern forms and some of the primitive forms, bear rough horn pads. There may be a similar pad on the frontals. The horns arising from these pads are characteristically two in number, one behind the other, but the arrangement varies. The horns are strong, epidermal structures arising out of close growing tufts of hair. In the horned forms, the nasals are heavy and broad and may be supported by a mesethmoid. In the hornless forms, they are narrow. The nasal apertures reach as far back as the first molar.

Dental formula:

$\frac{3-0}{3-0}, \frac{1-0}{1-0}, \frac{4-2}{4-2}, \frac{3}{3} = 44$ or 28 or 20

Incisors and canines frequently lacking. Premolars and molars more or less similar, being the same in the older forms.

Upper molars with thick cingulum, ectoloph and two oblique, weakly built transverse ridges, bound with the ectoloph.

Lower molars with two right-angled ridges to which the metaloph is attached by its anterio side. $M\frac{3}{3}$ without a third lobe.

Extremities usually short and plump. Radius and ulna strong and complete as in the Tapirs.

At least in the older forms, the carpus is the same as in the tapirs. Of the metacarpals, mc III is stronger than McII and IV. Mc V is short. Tarsus and metatarsus narrow in the primitive forms, short and broad in the modern.

Forefoot with 3 or 4 digits, hindfoot 3.

The rhinoceridae are grazers (with one exception). They lived and still live in certain parts of the world, in marshy bottom lands. The exist today in tropical India, Sundainseln and Central Africa. Their fossil remains have been found beginning in the upper Eocene of Europe and North America. In the Oligo, Miocene and Pliocene, a great wealth of forms developed. In Miocene, they appeared in North Africa, and soon after in Asia. They last appeared in Europe in the Pleistocene, is North America in the Pliocene.

Subfamily 1. Hyracodontidae.

Skull short with sagittal crest and conspicuous periotic. Nasals projecting, and hornless.

Dental formula:

$\frac{3}{3} \frac{1}{1} \frac{4}{4} \frac{3}{3}$

Canine weak. Placed close to the chisel-like incisor 3, and separated from the cheek teeth by a diastema. Premolars either heterodont or nearly homeodont.

Neck long& Extremities long and slender. Forefoot 4 to 3 digits, hindfoot 3.

Upper Eocene and Oligocene of North America.

Subfamily 2. Amynodontinae.

Skull in front of the orbit deeply hollowed. Fore-end of the snout broad. Nasals very short and hornless.

Canine above and below much stronger than the incisors, fanglike. Molars the same as Rhinoceros. Upper molars without . Premolars much smaller than the molars, but molariform.

Forefoot 4, hindfoot 3-toed.

North America Upper Eocene and Oligocene. Europe in Oligocene.

Subfamily 3. Rhinocerinae

*Genus Trigonias

Dental formula

$\frac{3}{3}\ \frac{1}{0}\ \frac{4}{4}\ \frac{3}{3}$

Upper incisor 1 and lower incisor 2 very much larger than the rest.
Premolars very much the same as molars.
Nasals long.
Forefoot 4-toed.
Oligocene White River

Characteristics of subfamily Rhinocerinae.

Dental formula

$\frac{3-0}{3-0},\ \frac{1-0}{0},\ \frac{4-3}{4-3},\ \frac{3}{3}$

Skull elongated. No sagittal crest
Periotic not on the outside of the skull.

Upper canine always strong, lower always absent. Incisors reduced in earlier forms, lacking later. Incisor 1 and incisor 2 greatly specialized. Upper cheek teeth with cingulum and two oblique transverse ridges. Upper and lower premolars frequently molariform.

Neck short. Extremities plump. Forefoot 4 or 3 toed. Hindfoot 3.

* Insert genus Trigonias

Genus Aceratherium

Dental formula

$\frac{2-1}{2-1}\ \frac{0}{0}\ \frac{4}{4}\ \frac{3}{3}\ \frac{3}{3}$

Upper incisors compressed. Lower incisors weak. Incisor 2 long, with three-cornered edge. Premolars always molariform. Upper premolars and
lars originally with only an antecrochet.
orefoot 3-toed, sometimes with short, slender 4th finger.
gocene 2hite River
ene, Colorado
Miocene Europe
India, Siwalik and China
rom Middle Eocene, upper Miocene, Lower Pliocene

rium

lways molariform.
having two transverse horn pads.
1 and bore two horns side by side at the end of

John Day Lower Miocene; Miocene of Nebraska.

Genus Teleoceras

Dental formula

$\frac{1.0.4.3.3}{1.0.3-2.3}$

Dentition very nearly similar to the modern. Two tusk below, and between these, a pair of small incisors. Cheek teeth more or less hypsodont. Skull brachycephalic, nasals thin, with a single small horn at the tip. Extremities very short.

North America, upper Miocene and Lower Pliocene.

Genus Aphelops

Similar in every respect to Teleoceras, except there is no horn.
North America: Upper Miocene and Lower Pliocene.

Genus Peraceras

No upper front teeth. Grinding teeth similar to those of existing species, but simpler -- less development of accessory spurs.
In other respects similar to Teleoceras and Aphelops.
North America: Lower Pliocene.

Subfamily 1. continued

Genus Hyrachus

A generalized and relatively undifferentiated type, ancestral to Hyracodon, and a possible ancestor of any of the perissodactyls except the horses and titanotheres.

Incisors all present, well developed and functional, tho not large. Canines moderately enlarged, forming small tusks. Premolars smaller than molars the molariform. The lower molars were identical with those of the tapirs; the upper molars showed a likeness to the rhinoceroses. Upper premolars 3-lobed. 4 premolars present on each side above and below. $P\frac{4}{4}$ has two ridges uniting internally to form a crescent.

Skull long, narrow and low. Nasal slender and thin. No horns. Neck short. Body long. Limbs of medium length and weight; slightly stouter than those of Triplopus of the upper Bridger and Uinta beds. Feet slender and particularly elongate. Manus 4 digits, pes 3.

Middle Eocene, Bridger and Wind River, of Wyoming.

Genus Hyracodon

This genus is tho to be intermediate between Hyrachus and higher members of the family Rhinoceridae.

They were entirely different in appearance and proportions from true rhinoceroses. Lightly built, slender and cursorial. Bore somewhat similar relation to horse as did the lophiodonts to the tapirs. Taller and heavier than a sheep.

Skull short, deep, and thick. Neck long, but with stout cervical vertebrae. Hornless.

Teeth low-crowned, and Rhinoceros-like in pattern, tho last upper molar had not perfectly acquired the triangular form characteristic of true rhinos. All premolars except the first were molariform tho very slightly smaller than the molars.

The anterior teeth, incisors and canines were quite different from the true rhinos. Small, with simple, pointed, and slightly recurved crowns, all about th same in size and form.

Body elongate, tho not massive. Limbs proportionately longer than in any rhinos, tho the limb bones were unquestionably like those of the rhinoceroses. Feet long and narrow, approximating in proportions those of the White River horses, Mesohippus.

Both fore and hind feet 3-toed. Third digit greatly enlarged, and lateral toes much reduced, tho still functional, strongly suggesting a resulting monodactyl foot, had not the subfamily become extinct.

Oligocene White River.

Metamynodon

Dental formula

$$\frac{2}{2}, \frac{1}{1}, \frac{3}{2}, \frac{3}{3}$$

Very high crowns, strongly compressed.

Tusks present

Hornless. Short-necked. Skull modified so as to resemble that of a carnivore.

The animal was large, heavy, and shortlegged. Probably amphibious.

Oligocene -- White River Dakota.

The Pleistocene of North America

Conditions of life in the Pleistocene were more or less based upon the climatic conditions, which in turn were associated with the changes in level of the land with the sea and with the periods of glaciation.

The period of elevation began in the late Pliocene and extended late into glacial times. This was followed, in post-glacial time, by a period of depression, which was, in turn followed by a reelevation to the present levels.

Elevation in British Columbia resulted in a rise of from 3,000 to 5,000 feet above what it is at present. On the eastern coast of the United States, Maine rose 1,000 feet, and the coast to New York 150 feet accompanied in the glacial regions with the formation of channels and fjords. California was 2,000 to 3,000 feet above its present level and there were deep canyons eroded in the Sierra Nevadas and Coast Ranges. During glaciation of this coast the glaciers came down over canyons 6,000 to 7,000 feet above sea level, something as in the Olympic penninsula of Washington today. From this evidence it is probable that the Pleistocene climate of California during elevation was similar to that at Olympic penninsula today -- cool and rainy and forested by conifers. The Channel Islands were at this time a part of the main land, affording a passageway for mammals. In Alaska the coast was elevated so as to form a broad land bridge with Asia.

The depression which followed affected both the Atlantic and Pacific coasts, carrying the northern shores several hundred feet below what they are today. This period was warm and moist.

The reelevation which followed, affected both coasts, bringing them to their present levels.

Osborn holds to the view that glaciation took place in five separate

periods separated from one another by interglacial periods of climatic conditons similar to those of today. The periods are as follows:

The Sub-Aftonian glacial epoch comparable to the Gunz glaciation of the Alps, followed by the first interglacial period, the Aftonian, which is of importance in its deposits, the Aftonian gravels of Iowa, which furnish a rich fossil mammalian fauna. This fauna together with the buried forests extending over Iowa, giving evidence of a luxuriance of forest growth, indicates a warm and probably very moist period. The second glaciation, the Kansan, is comparable to the Mindel and Saxonian of Europe and was probably the period of maximum glaciation in Iowa; the Yarmouth Interglacial which followed, was, according to evidence, the longest of the interglacial periods, having forests and terrestrial faunas as in the Aftonian. The third glacial, the Illinoian, was chiefly from the northeastern Labradorian center and only covered a small part of Iowa; the Sangamon Interglacial following, was shorter than the Yarmouth, but is well indicated by buried forests, pond silts, and peat beds containing quantities of tamarack roots, etc, and was probably of long duration. The fourth, or Iowan Glaciation was of less extent than the preceding periods, barely reaching Iowa; the Peorian Interglacial following, was short; the deposits contain terrestrial molluscs. The last glaciation, the Wisconsin, has been divided into Early and Late Wisconsin. One sheet extended into Iowa. This glaciation sent the "great terminal moraine" across the continent.

With the advance and retreat of the glaciers, there was a corresponding southward and northward movement of the rain belt, resulting in periods of moisture and periods of aridity particularly notable in the Great Basin Region. This is evidenced particularly in the strata marking the rise and fall of Lake Bonneville and of Lake Lahontan. Lake Bonneville was the ancestor of the Great Salt Lake of today, and at its

maximum is estimated to have covered an area of 19,000 square miles and to have been 1,000 feet in depth, contrasted with the present 50 foot depth. Lake Lahontan is estimated to have covered an area of 9,000 square miles. As the second period of rise in these lakes shows remains of mammalian and bird life, Osborn emphasizes the necessity of correlating this rise with one of the five glacial epochs.

Another important evidence of changing climate is found in tracing the migration of both flora and fauna. Examples are as follows:

The flora of the Sangamon Interglacial in Toronto is quite similar to that found in Virginia today, indicating a temperature during the Sangamon like that of our Middle and Southern States today prevailing as far north as Ontario.

Over this Sangamon flora are found the cold climate fossil flora indicating a return to temperature like that of southern Labrador and northern Lake Superior.

The fossil tamarack is found in Georgia, 480 miles south of its present limit.

Of the animals, we find remains of the Northern walrus, Odobaenus, as far south as Georgia, and remains of the southern manatee, Manatus, as far north as the coast of New Jersey. Other northern animals found to have migrated southward are the caribou, Rangifer, in Ohio, the moose, Alces, south of the Missouri riber, the wapiti, Cervus canadensis, in Florida.

Migration of the birds also, is of course noted, and Allen is of the opinion that this forced migration in the waning of the glacial period, when certain areas were attractive in the summer, but still r etained the cold winters, thus dirving the birds south, established a habit of migration which has become hereditary.

The Pleistocene of America is of importance because of the fact that it presents for the first time the life of all regions of the United States, from the plains and mountain region of the West, of the Pacific slope, of the forested parts of the east quite unknown before, of the sandy savannahs of the south and also many portion of British Columbia and Alaska. Beside being of such great extent, geographically, the animal assemblage itself is very large and varied. It includes: the mastodon and many elephants, as Osborn says, quite as majestic as those of the Old World; great herds of llamas, camels and troops of horses; tapirs; no true cattle, but many widely distributed species of bison; the ground sloths of giant size , and the great armored glyptodonts; and, of the carnivores, the distinctive saber-tooth cat, as well as many true cats and various species of Canidae.

Osborn states that tho this great extension and assemblage enhances the interest and possibility of knowledge, it at the same time, offers many difficulties in correlation -- of the faunas east and west of the Sierras and Rocky mountains, and on a larger scale, with the fauna of the Old World.

The richest deposits of the Pleistocene of America are found south of the farthest advance of the glaciers, and only in the Afton formation of Iowa and the Toronto formation of the Don Valley, has a mammalian fauna been located between two series of glacial deposits. This leads to a necessity of dependence on other evidence beside correlation with glacial deposits to mark the progress of the Pleistocene, and thus establish a correlation between the faunas of the east and the west and between the Old World and the New. For this reason Osborn has suggested the division of the Pleistocene into faunal zones based upon the following plan:

1. The survival of characteristic Pliocene types.

2. The extinction and emigration of these older types
   Note on extinction:- The extinction of the old types present at the beginning of the Pleistocene was contemporaneous with the Glacial Age. Glaciation brought about changes in temperature and moisture which Osborn states were <u>indirectly</u> the cause of this extinction. Herds of animals that could not withstand the cold were reduced in number. This reduction caused the herd to be more easily attacked, there not being a suffident number of adults to protect the young; this would in time lead to extinction. The cold may also reduce the food supply and cause the death of young which in the northern latitudes are born in the spring. Deforestation, due to glaciation, is also of importance in extinction. Many animals dependant on the forests for food and shelter, would become diminished and finally extinct if deprived of the forests.
   Increased rain-supply may also cause extinction to another type of animals than those influenced by the cold. This is due to the increased moisture bringing with it: a diminution of the harder grasses to which certain quadrupeds have become adapted; the production of new poisonous plants; the introduction of new insects and other pests, correlated with an introduction of Protozoan diseases; the erection of new forest barriers to migration.
   Thus with this brief summary of the indirect effects of climate on extinction of animals, we can more readily correlate the faunal zones with the climatic changes as they occurred in the Pleistocene.

3. The arrival of types new to America, from the Old World.

4. The comparison of the climatic adaptations of New World forms with those prevailing during the four zones of mammalian life in Europe.

The faunal zones are:

I. The Equus-Mylodon Zone of the Plains Region.

This is divided into an Early and a Late Equus Zone based on the probable overlapping of the Late Zone with the second or Megalonyx Zone. In the Early Zone the following types were charadteristic:

Horses, abundant
Camels and llamas, abundant
Columbian mammoths, abundant
Imperial mammoth, in the south, and questionably in the north
Prong-horn antelopes, on the Great Plains -- the first
Capromeryx, the last of the Merycodonts
Platygonus, several species
Mylodont sloths, abundant in the west and south
Glyptodonts, in the south
Casteroides, the giant beaver, first appears
Taxidea, the badger, first appears
Saber-tooths numerous -- no other large felines
Dinocyons, doubtfully present

This zone differs from the Late Equus Zone and the Megalonyx Zone in the absence of Bison and Megalonyx.

II. THe Megalonyx Zone.

The climate of this zone was evidently more temperate than of the preceding zone as evidenced by the rich forest and meadow fauna. It is as follows:

Megalonyx, characteristic in all deposits
Megatherium, abundant
Bison, widely distributed
Columbian mammoth, now limited to the west and southeast
Mastodon, abundant in the east, rare in the west
Horses, fairly abundant
Tapirs, in forests of east and southeast, none in the west
Llamas confined to the west, no longer present in the east
Alces, the moose, present in the west
Odocoileus, the deer, abundant
Mylohyus, replaces Platygonus in later deps
Euceratherium and Preptoceras, relatives of the musk ox, in the west
Oreamnos, in the later deposits of the west
Tree porcupines, widely distributed
Giant beaver, not in the south
Smilodon, widely distributed
Felis atrox, in the west and southwest
Ursus and Arctotherium, widely distributed

III. The Ovibos-Rangifer Zone of the plains and forests, corresponding to the last glacial advance and including mammals typical of the colder regions and hitherto absent in America. The musk ox is characteristic, Reindeer are present, and Cervus, the Old World deer. Mylodon, Megalonyx and the Tapirs and probably the llamas are all absent. As indicated by the name, Ovis, the mountain sheep, and Rangifer, the caribou are present.

IV. The Cervus Zone of the forests of the East and West, of the prairies and the great plains arid region. The Old World deer, Cervus canadensis, is characteristic and widely distributed. The fauna is that found by the early settlers of this continent; horses, tapirs, and proboscideans had disappeared.

The fauna of the deposits of the west is for the most part in the second zone, as may be seen from the fauna listed above for that zone.

The fauna of Fossil Lake deposits of Oregon, is, as Osborn point out, probably of the Early Equus Zone.

Hildegarde Howard

The Pleistocene of North America
from Osborn's
Age of Mammals

Paheontology 104

Camelops Compared With Auchenia and Camelus

In Camelops the general outlines of the skull resemble Auchenia more than Camelus, the frontal region of the latter being rather broad.

The rostral region tapers more gradually toward the anterior end than that of Camelus. In this respect it again resembles Auchenia.

The frontal region in both Auchenia and Camelus is concave. According to Merriam it is convex in Camelops, but from the specimens available the region appeared to me to be straight.

The orbits are relatively far back, the anterior border being above the last upper molar. In Auchenia and Camelus this border is above the middle of M2.

The basicranial and basifacial axes are nearly paralell as in Camelus.

The nasals are long and narrow with posterior ends separated by a wedge of the frontals. The outer borders do not spreadx widely as in Auchenia and Camelus. The nasals of Auchenia are quite short and broad.

The anterior ends of the nasals are in broad contact with the premaxillaries. This also true of Auchenia. The notch for the posterior border of the anterior narial opening is not behind the posterior ends of the premaxillaries as it is found to be in the two other forms. The anterior ends of the nasals project forward beyond the superior border of the premaxillaries -- again unlike either of the other forms, though Auchenia is more nearly similar in this respect than is Camelus.

A large deep fossa is present near the upper margin of the maxillaries over Pm4, its inferior margin not being strongly marked. Merriam says there is no suggestion of this fossa in either Auchenia or Camelus, but in the specimen of Auchenia available, there seems to be a slight indication of it.

The zygomatic process of the squamosal extends forward well beneath the posterior border of the orbit. Merriam states that Auchenia

exhibits this character to a certain extent; but though the anterior extension of the process is somewhat greater than in Camelus, it does not come beneath the border of the orbit in the specimen here available.

The jugal is thicker vertically than it is in Camelus and shows an inferior crest not present in Camelus, but exhibited to some extent in Auchenia.

The palate is narrow more as in Auchenia than in Camelus and longer relatively than in either of the other forms.

The basi and presphenoids form a deep narrow ridge, differing in this respect from the other forms. Camelus shows a slightly greater tendency in this direction than does Auchenia. The inferior processes of the alisphenoid are smaller and do not project as far inferiorly as in Camelus. Auchenia is similar in this respect.

The postglenoid process is relatively larger than in Auchenia, though not so large as in Camelus. It projects laterally further from the mastoid than in the other forms.

The mastoid resembles that of Auchenia more than Camelus in being deep, narrow, and relatively straight whereas that of Camelus is bent slightly anteriorly and is hollowed out to admit the postglenoid process which is close against it. The mastoid and paroccipital process are closer together than in the other forms.

The supraoccipital is similar to that of Camelus, but quite different from that of Auchenia in which there is a decided median ridge with a deep fossa on each side. In Camelops and Camelus, this condition is not shown -- the center region being depressed with lateral risings on either side. The region above the foramen magnum is slightly convex as in Camelus, while in Auchenia it is strongly convex to angular.

The infraorbital foramen is divided by a bridge of bone into a large

and a small foramen. In Camelus and Auchenia there is no such division.

The anterior palatine foramina extend back to the canines. They do not extend this far in either of the other specimens. The maxillaries extend to the anterior border of these foramina -- again unlike Auchenia or Camelus.

The anterior mental foramen is situated about on a line with the lower canine as in Auchenia. In Camelus it is situated somewhat farther posteriorly.

The mandible:

The symphysial region is relatively short as in Auchenia. It is somewhat longer in Camelus.

The symphysis is shorter than in Camelus though relatively slightly longer than in Auchenia.

The ramus is relatively higher than in either of the other forms, though Auchenia resembles it more nearly in this respect.

Dentition:

The dental formulae of Camelops and Auchenia are the same: $\frac{1\ 1\ 2\ 3}{3\ 1\ 1\ 3}$. That of Camelus differs in the number of premolars, being three in the upper jaw and varying in the lower, both 1 and2 being present on one ramus, while both are absent on the other, or other possible combinations.

The dentition as a whole shows greater resemblance to that of Auchenia. The styles on the outer side of lower molars 2 and 3 present in Auchenia, are, however, lacking in Camelops. On the basis of this character Wortmann separates Auchenia and Camelops.

Camelops shows greater resemblance to Auchenia than to Camelus. Characters giving evidence of this fact are:

1. General shape of skull

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  BLvl:  m     Form:         Conf:  0     Biog:          MRec:         Ctry:  ctu
               Cont:  bc     GPub:        LitF:  0       Indx:  0
  Desc:        Ills:  ab     Fest:  0     DtSt:  s       Dates: 1968,      ¶
▶   1  010      68-29321 ¶
▶   2  040      DLC ǂc DLC ¶
▶   3  050 00   E59.A7 ǂb W3 ¶
▶   4  082 00   739.2/27/17498 ¶
▶   5  090      ǂb  ¶
▶   6  049      CNHM ¶
▶   7  100 1    Wardwell, Allen. ¶
▶   8  245 14   The gold of ancient America, ǂc by Allen Wardwell. ¶
▶   9  260      Greenwich, Conn., ǂb Distributed by New York Graphic Society ǂc
[c1968] ¶
▶  10  300      156 p. ǂb illus. (part col.), map. ǂc 23 cm. ¶
▶  11  500      Catalog of an exhibition shown Dec. 5, 1968-Jan. 12, 1969, at
the Museum of Fine Arts, Boston; Feb. 1-Mar. 9, 1969, at the Art Institute of
Chicago; and Mar. 24-Apr. 20, 1969, at the Virginia Museum. ¶
▶  12  504      Includes bibliographical references. ¶
▶  13  650  0   Indian art. ¶
▶  14  650  0   Indian goldwork. ¶
▶  15  710 2    Museum of Fine Arts, Boston. ¶
▶  16  710 2    Art Institute of Chicago. ¶
▶  17  710 2    Virginia Museum of Fine Arts. ¶
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2. Rostral region tapering gradually to anterior end.

3. Anterior end of nasals in broad contact with premaxillaries.

4. Fossa near upper margin of maxillaries.

5. Shape of jugal.

6. Palate narrow.

7. Size and shape of inferior processes of alisphenoid.

8. Size and shape of mastoid.

9. Position of mental foramen.

10. Length of symphysial region

11 Length of symphysial union

12 Height of ramus

13 Dental formula

14 General character of dentition.

Hildegarde Howard

Palaeontology 104B

Camelops Compared With Auchenia and Camelus

A

Diagnostic Characters of Animals from Rancho La Brea

Felis daggetti

Type specimen,-- mandible from Rancho La Brea.

The specimen represents Felis daggetti as an animal of equal, or probably greater size than the modern Puma.

Compared to the Recent puma of California, the mandible, though of approximately the same dimensions as the Recent form, shows greater width of the angle and an unusual backward slant of the coronoid process. The dentition is much more massive than in the Recent form, and the posterior portions of $P\frac{3}{}$ and $P\frac{4}{}$ are very wide.

The anteroposterior diameter of $P\frac{4}{}$ is relatively short in comparison with the jaguar forms. Felis daggetti is evidently more closely related to the puma than to the jaguars. It differs widely from Felis atrox with which it is associated, and ~~differs~~ represents a species quite unlike any other species heretofore ~~d~~described in North America.

Felis atrox bebbi

Type specimen of Felis atrox,-- portion of lower jaw from near Natchez, Mississippi.

Type specimen of Felis atrox bebbi,-- skull and mandible from Rancho La Brea.

Felis atrox bebbi from Rancho La Brea is evidently of the same species as Felis atrox described by Leidy from a single ramus of a lower jaw taken near Natchez Mississippi. There are, however, certain slight differences, such as the size of the canine, the form of $P\frac{3}{}$, the length of the diastema and the form of the symphyseal region, which have led to the placing of the Rancho La Brea specimen in a separate variety.

There is also some controversy as to its relation to F. imperialis

described by Leidy from Livermore Valley. The latter form is much smaller, but it is thought that the size may be due to individual variations.

Felis atrox bebbi is remarkably like the African lion of today. The width of the muzzle compared to the length is five per centless than in the modern lion, while the transverse diameter of the muzzle is five per cent greater.

The individuals of this Pleistocene form were very large. The canines relatively large, the incisors small or set in a comparatively narrow space. In the mandible the coronoid process is high and wide and near the medial end of the condyle. The masseteric fossa beside being wery deep has a marked forward extension to the middle of the inferior carnassial. The angle is produced inferiorly rather farther than in the lion and tiger. In the cranium, the postorbital processes of the frontal are relatively far back. The brain case is small, also the auditory bullae. The occiput is high and narrow.

Canis occidentalis furlongi

Type specimen,-- skull from Rancho La Brea

The Pleistocene timber wolf, Canis occidentalis furlongi differs subspecifically from the modern gray timber wolf. The nose is narrower, the superior carnassial more massive, and M2 relatively narrower anteroposteriorly.

The skull is smaller and narrower than that of the large dire wolf, Aenocyon dirus. The nasals are long. The postorbital processes of the frontal are small and the sagittal crest is low.

All the material from Rancho La Brea referred to Canis occidentalis furlongi is evidently of a single form, though presenting noticeable variation in the size of the teeth.

This wolf is rare in the deposits compared to the dire wolf and also

is less common than the coyote, Canis ochropus orcutti.

Canis ochropus orcutti

Canis ochropus orcutti is closely related to the modern coyote, living in southern California. The difference lies in the size of the skull. In the Pleistocene form the skull is broader acress the palate and zygomatic arches, while the mandible is higher and thicker transversely. The teeth of the fossil from do not differ widely from the modern Canis ochropus, the carnassials, however, being somewhat heavier. The skeleton as assembled from parts of different individuals indicates the same slender-legged, fleet-footed type as today. There is slight evidence, based on fragmentary specimens differing slightly from Canis ochropus orcutti, that Canis ochropus was also present in the Pleistocene though to no such great extent as the characteristic Pleistocene form.

Canis ochropus orcutti, though found in rather large numbers, cannot compare in abundance, with forms of the Aenocyon dirus type.

Canis andersoni

Type specimen,-- skull from Rancho La Brea

The type specimen is the only representative of Canis andersoni. It is a short skull, with a short and broad muzzle,-- the breadth being about equal to that in Canis ochropus, but relatively shorter. The superior carnassials are the only teeth preserved. They are slightly thicker than those of Canis ochropus, though otherwise of about the same size.

A satisfactory comparison of this form can hardly be made at this time, owing to the scarcity of material.

Bison antiquus

Type specimen,-- horn core from Big Bone Lick, Kentucky.

The breadth of the skull and the horn cores of Bison antiquus is relatively greater than in the modern speices, The length, however, is about the same. In Bison antiquus the breadth of the skull is one and a third times that in the corresponding sex of the existing forms. The orbits are the same. The nasal bones ane relatively shorter and broader, and less arched; they taper gradually to the tip. The horn cores are longer and more slender, those of the females of B. antiquus being about equal in length to those of the male of B. bison, tho, of course, very much more slender. The horn cores of the males of B. antiquus are stouter than those of B. bison.

The angle of insertion of the horn-cores is one of the most characteristic characters of B. antiquus for instead of making an obtuse angle with the median line of the face as in B. bison, they are inserted almost at right angles. The curvature of the horn-cores is, however, about the same as in the existing types.

In general the teeth of B. antiquus have a more complicated enamel pattern than those of B. bison. The upper teeth, too, are larger than in the modern form. The individual variation in the species B. antiquus, as well as in the other forms, is so great that it is hardly possible to give a difinite statement as to characteristic structure or size.

The individual and sexual variation within the species B. antiquus as evidenced in the size of the horn-cores and skull is approximately the same as in the modern species. B. antiquus is well represented in the Rancho La Brea deposits, many almost perfect skulls having been found. This form was evidently wide ranging, as evidenced by the specimens found throughout the United States.

Platygonus n.sp. or subsp.

Type specimen -- astragalus, from Rancho La Brea.

The material of Platygonus from Rancho La Brea consists of an astragalus found by the University of California, a fragmentary skull and superior dentition, and a few skeletal parts found ~~kxx~~ by the Los Angeles Museum.

The skull in the Los Angeles Museum collection posesses only the facial region and the superior dentition in a well preseved condition. The cranium proper is badly mutilated. The specimen does, however, certainly belong to the genus Platygonus. In size this skull is about that of P. compressus. The size and also certain fossae appear to link the Rancho La Brea form with P, Leptorhinus from the Pleistocene of Kansas.

The diastema between the superior canine and Pm 2 though slightly longer than that in modern Tayassu is much shorter than that of any other form of Platygonus from the Pleistocene of North America and thus in this respect approaches the modern form.

In fundamental characters the teeth of the Rancho La Brea Platygonus resemble those of P. leptorhinus and P. compressus. There are minor differences in size and shape.

In spite of the strong resemblance of Platygonus to P. leptorhinus and P. compressus, it is thought that it may be a distinct species or at at least a distinct subspecies.

Nothrotherium

There are about eight complete crania and fragments of four others, with a number of mandibles and other elements of the skeleton, and one nearly complete skeleton of Nothrotherium from Rancho La Brea in the posession of the Los Angeles Museum.

Of the three types of ground sloths found at Rancho La Brea, Nothrotherium is the smallest, only one skull -- the largest -- being about as long as one of Megalonyx jeffersoni, all other specimens are shorter Aside from the shortness of the skull, however, a marked distinction is shown also in its slenderness, making the anterior aspect of the skull of Nothrotherium decidedly different from that of Megalonyx. This slenderness of skull is found also in the Miocene Megalonichids of the Santa Cruz. This and other characters have led to the idea of the descent of Nothrotherium from Hapalops. _ Megalonyx shows greater difference from the Miocene types than does Nothrotherium. The two Pleistocene forms are probably related prior to the Miocene, coming up in two genera already separated in the Santa Cruz Miocene. This view is held by Scott and Ameghino.

Nothrotherium of Rancho La Brea is probably identical with N. shastense of Potter Creek Cave, as stated by Stock.

The lower jaw of Nothrotherium is very similar to that of Hapalops and in this respect, again resembles the Miocene form more than Megalonyx, being more slender than that of the latter.

Nothrotherium posesses reduced dentition and smaller teeth than the Miocene Megalonichids and Megalonyx.

In the Rancho La Brea deposit Nothrotherium is found much more abundantly than Megalonyx and not nearly so abundantly as Mylodon, though Megalonyx seems to be a form of wider range. Nothrotherium evidently flourished in the region of California and Texas during part of the Pleistocene. It may be found to be of even wider range.

Hildegarde Howard
Palaeontology 104B

Diagnostic Characters of Animals from Rancho La Brea

Hildegarde Howard -

The Canidae of Rancho La Brea

There are six types of Canidae represented in the asphalt deposits of Rancho La Brea; the most abundant being the large dire wolf, Aenocyon dirus, Leidy which represents overfifty per cent of the total number of specimens. Second in abundance, though in no measure equalling the representation of dire wolves, is the coyote group, Canis ochropus orcutti Merriam. The other forms, Canis occidentalis furlongi Merriam, Aenocyon milleri Merriam, Canis andersoni Merriam, and the fox group, Urocyon californicus Mearus are quite rare.

The type specimen of Aenocyon dirus is from the Pleistocene beds of the Ohio River in Evansville Indiana. Other specimens have been found in Texas; in California in the Quaternary deposits in Livermore Valley; in the Tulare asphalt deposits; in the lead region of the Upper Mississippi; in the Sheridan formation in Kansas; and, most recently, in deposits in Tequixquiac, Mexico.

Associated with these specimens of Aenocyon dirus there are, in the Indiana beds, such fossil forms as Megalonyx jeffersoni, Tapirus haysii, Equus americanus, Bison americanus, and Cervus virgianus; and in the Texas region forms such as Mylodon ? sodalis, Elephas primigenius, Equus excelsus and others which are unmistakably of Pleistocene origin. This association of Aenocyon dirus with other species from the Pleistocene is constant throughout the various other regions in which A. dirus is found, leading, of course, to the conclusion that A. dirus was also of Pleistocene age, though the actual period of its appearance and disappearance has not been determined.

As to the distribution of A. dirus, as far as actual specimens have been discovered, it was evidently a form which ranged widely

thruout North America, from the east to the west coast and from Mexico north as far as the Upper Mississippi. There is some supposition that the group may have extended into Canada, but this is uncertain. Possibly the timber wolves, Canis occidentalis furlongi, occupied the more northerly parts, contemporaneously with the maximum extent of the Aenocyon group in the Sonoran region. It is a noteworthy fact that as far as is known Aenocyon is not present in the deposits of Fossil Lake Oregon. There are found in that region a wide range of Pleistocene forms including wolves and coyotes, but no A. dirus. It would seem that if the form had been present in the Fossil Lake region in numbers at all comparable to the other regions, it would have left some trace. The supposition is that either Fossil Lake was too far north, or that the deposits there are of earlier, or possibly later period in Pleistocene than the deposits containing Aenocyon dirus.

The Aenocyon group includes two forms, Aenocyon dirus and Aenocyon milleri.

Aenocyon dirus is characterized by its massive skull and dentition, together with an extreme overhang of the inion and a shortening of the basicranial region posterior to the glenoid fossae. The upper and lower carnassials are extremely large and the hypocone of M 1 is reduced.

Aenocyon milleri has a smaller skull, with a low sagittal crest and a less prominent inion. The nasal processes of the frontal are very long. The dentition, as in A. dirus is massive. In M1, however, the hypocone is not reduced, but is unusually well developed, extending antero-internally around the protocone and connecting with the cingulum on the anterior side. The skull of A. milleri is intermediate between A. dirus and Canis occidentalis furlongi, being smaller than A. dirus and yet much broader than C. occidentalis:

The nasals are narrower posteriorly than those of A. dirus, but are broader and shorter than those of C. occidentalis.

Canis occidentalis furlongi differs from Aenocyon dirus chiefly in the form of M1, which in C. occidentalis furlongi is wide transversely, with the inner lobe narrow anteroposteriorly, and the hypocone large, extending around anterior to the protocone somewhat as in A. milleri.

In skull no. 19792 which has been referred to C. o. furlongi, there is a marked difference from A. dirus. The skull is both smaller and narrower, with long nasals, small postorbital processes of the frontals and a low sagittal crest.

Canis occidentalis furlongi from Rancho La Brea differs from the modern gray timber wolf, Canis occidentalis, in a tendency to narrowness of the nose and in the massiveness of the superior carnassial, and relative narrowness, anteroposteriorly, of M2. All the material from Rancho La Brea referred to C.o.furlongi seems to represent a single form, tho having noticeable variation in the size of the teeth. This form differs at least subspecifically from the modern form. This type of wolf was rare compared to the dirus type and also less common than the coyotes.

That the coyote group, Canis ochropus orcutti is not so abundantly represented in the asphalt deposits may be due in part to some higher intelligence which enabled individuals of this type to recognize danger, or to the lure of entrapped animals for food being less for the coyotes. The truth as to any higher intelligence on the part of the coyote can hardly be determined, though it is true that the brain in this form was relatively larger than that of the dire wolf. However, as to the lure of food, it is interesting to note that the small mammals and birds upon which the coyotes doubtless preyed are found in relatively much fewer numbers in the asphalt

than are the larger animals upon which the powerful dire wolves were enabled to prey. Even this fact, however, can only partially account for the great difference in numbers of the Aenocyon dirus group and the Canis ochropus orcutti group, and it is evident that the coyotes of this period were not as prevalent as the dire wolves.

Canis ochropus orcutti is closely related to the coyote living now in southern California, Canis ochropus; the difference being in the larger skull of the Pleistocene form. This skull is broader across the palate and the zygomatic arches, while the mandible is higher and thicker transversely. The teeth of the fossil form differ from those of the modern only in somewhat heavier carnassials. The skeleton as assembled from parts from different individuals shows the same characteristics of its slender-legged, fleet-footed modern relatives. From such fragmentary specimens as have been found slightly differing from C. ochropus orcutti, it would seem that Canis ochropus was also present at that time.

Canis Andersoni is represented by a single skull from the La Brea asphalt. This skull is short, with a short, broad muzzle, the breadth being about the same as that in Canis ochropus, but relatively shorter. The superior carnassials are the only teeth preserved, and these, though of about the size of those of C. ochropus, are slightly thicker. As the one specimen is all the material available on Canis andersoni, a satisfactory comparison with other forms can hardly be made at the present time.

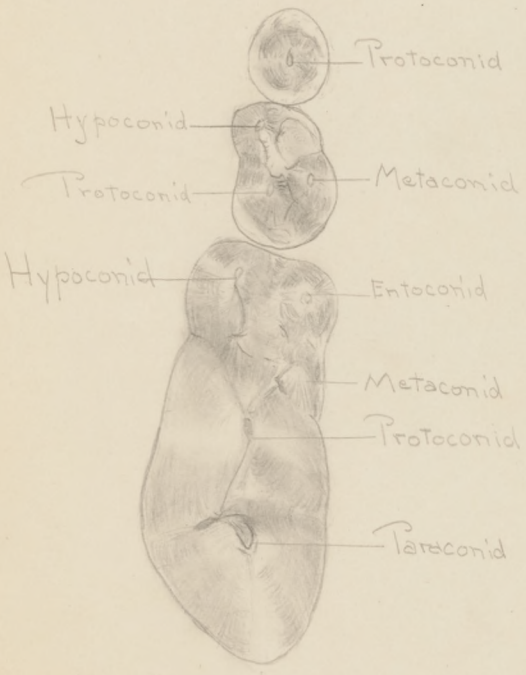
Urocyon californicus is a form which has undergone less modification from the Pleistocene to the present than any other canid group. The specimens as found in the La Brea asphalt are of similar size and character as two Recent specimens from the San Jacinto region and represent a form almost identical with the present fox of southern California.

Teeth

Right

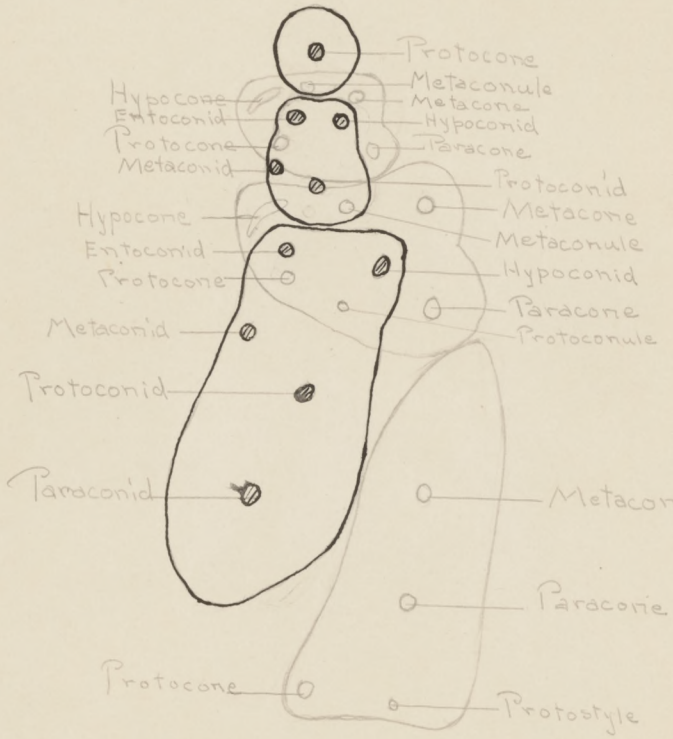
Upper Jaw
Pm 4, M 1, M 2.

Side view.



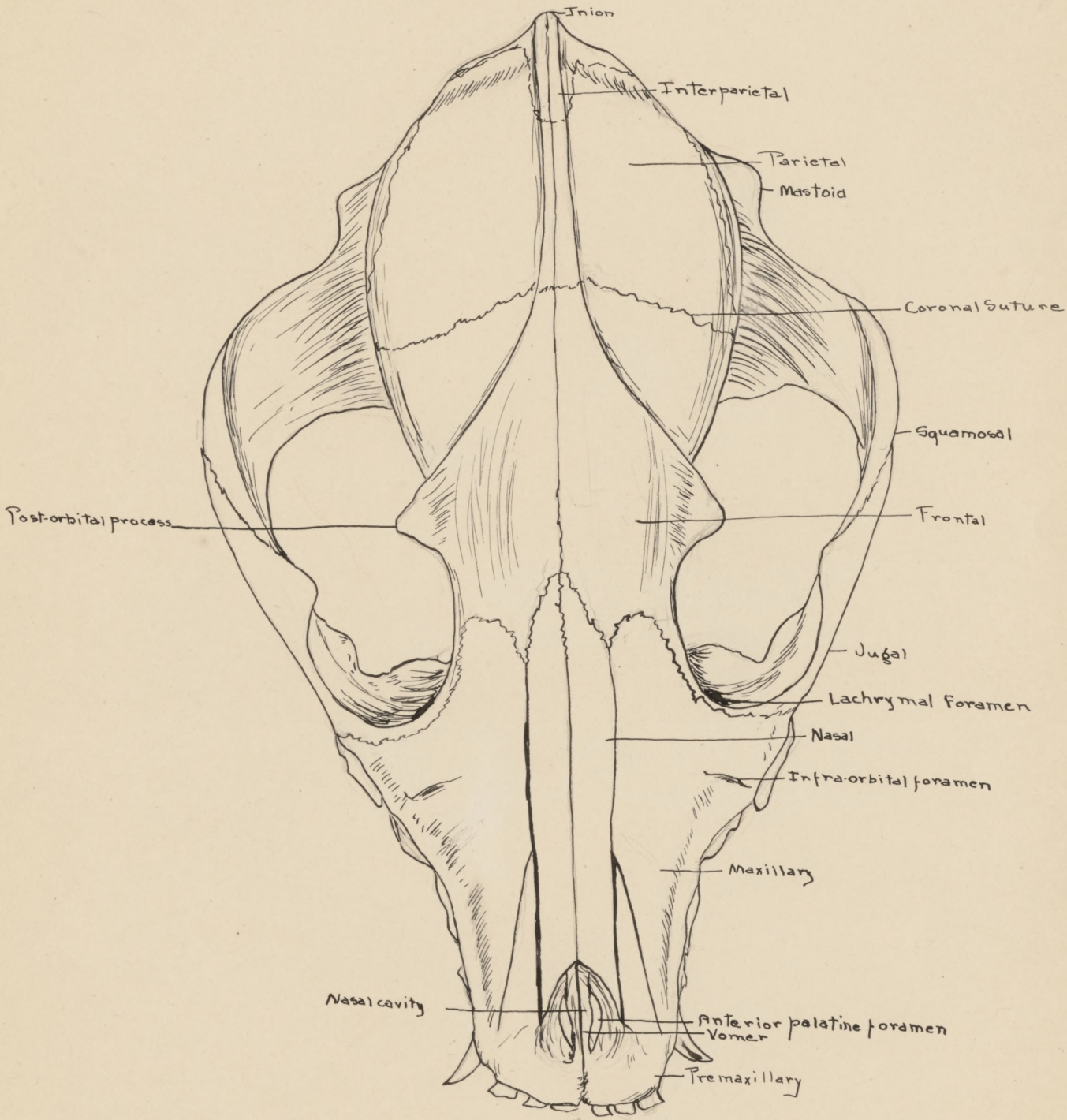
Right

Lowerjaw
M 1, M 2, M 3.

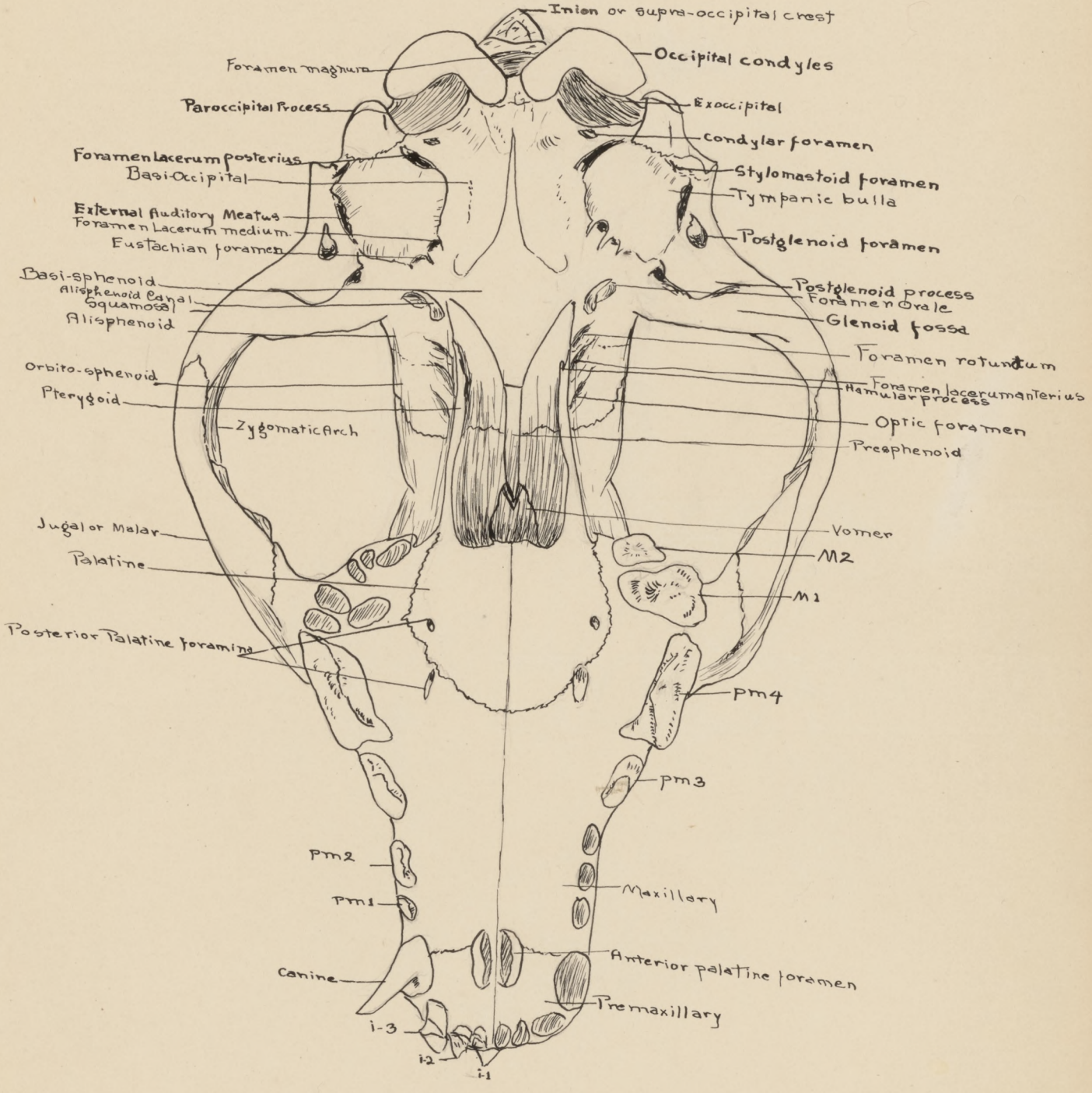


Lower jaw - ink
Upper jaw - pencil

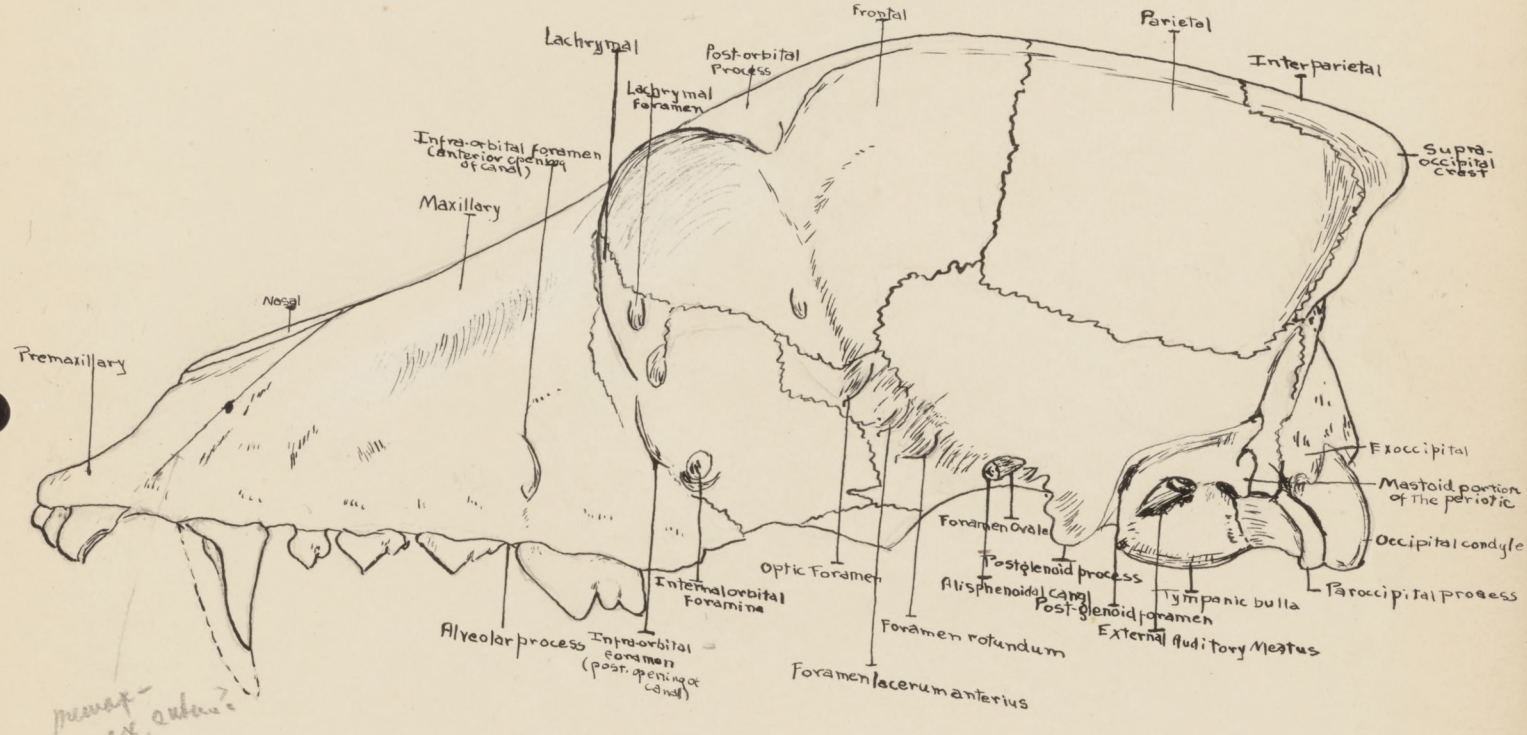
Diagram of occlusion of teeth
Pm $\frac{4}{4}$ M $\frac{1}{1}, \frac{2}{2}, \frac{3}{3}$



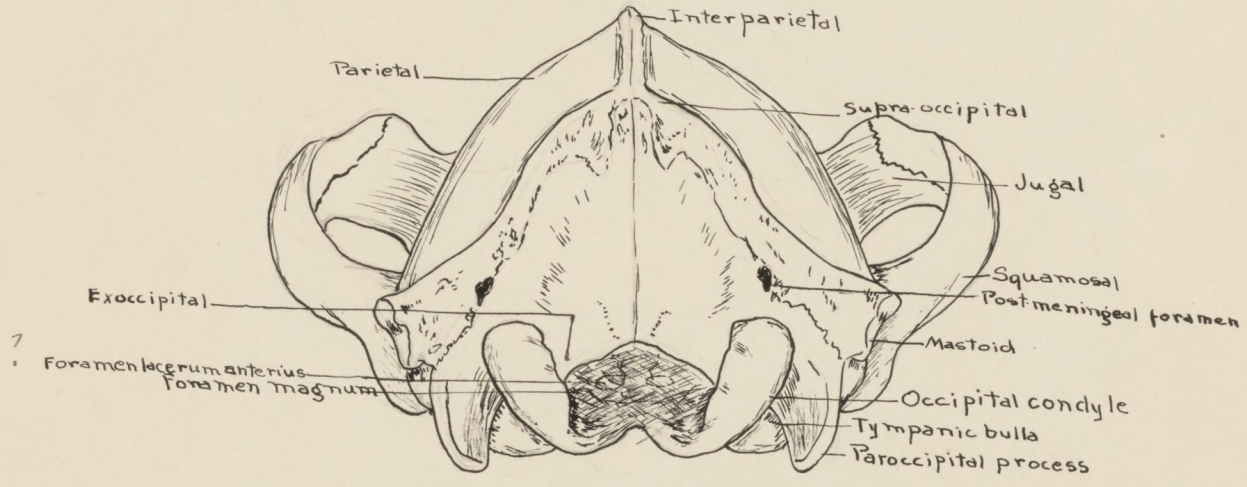
Dorsal view of skull



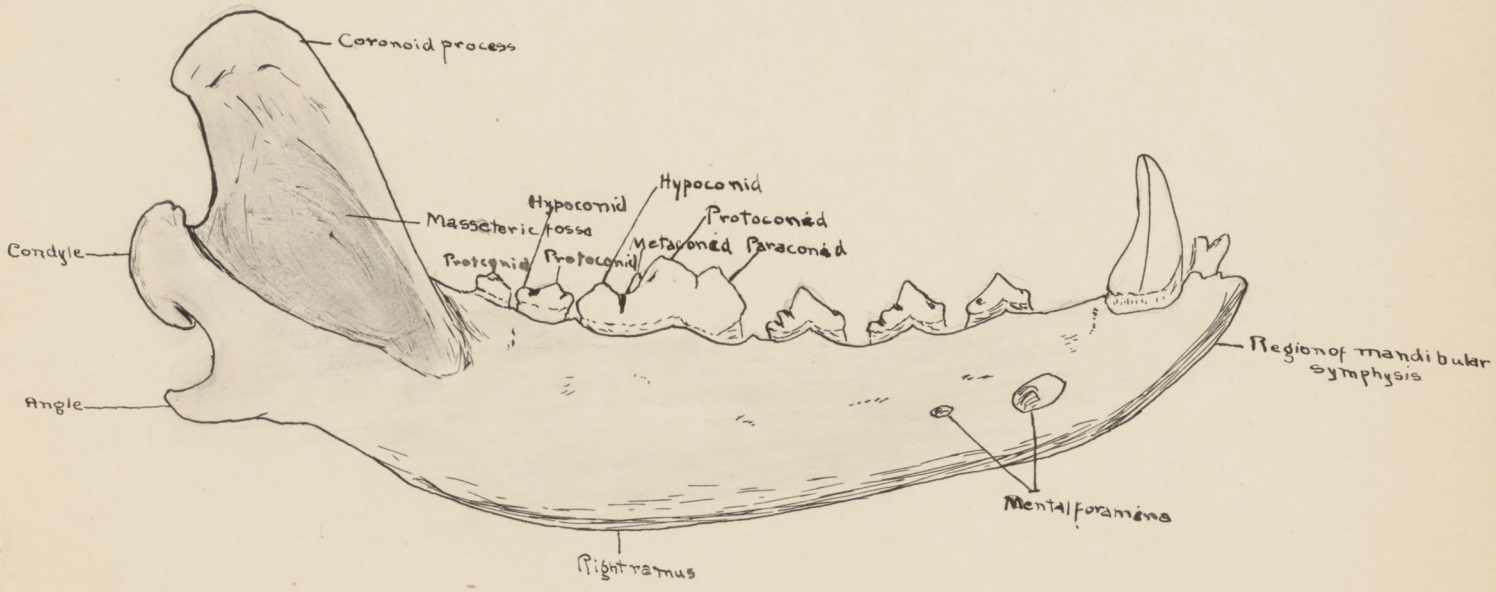
Ventral view of skull



Lateral view of skull



Posterior view of skull



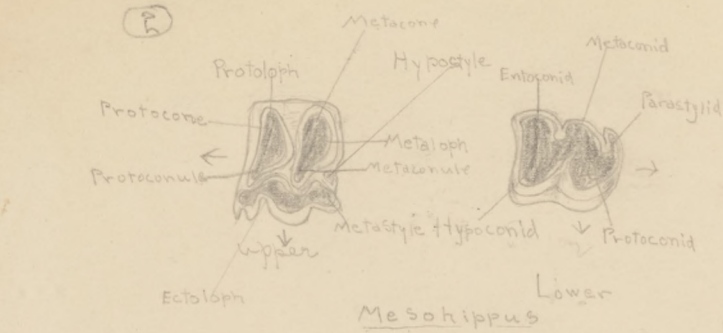
Outer view of right ramus

H. Howard

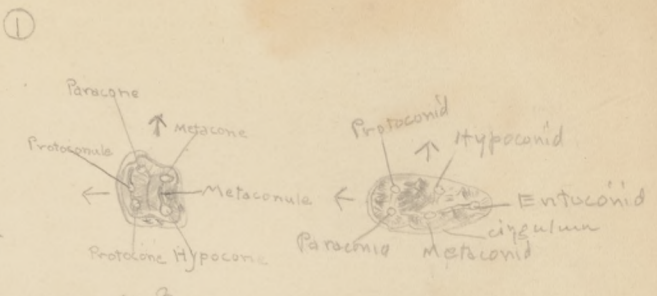
= dentine

= cement

= enamel

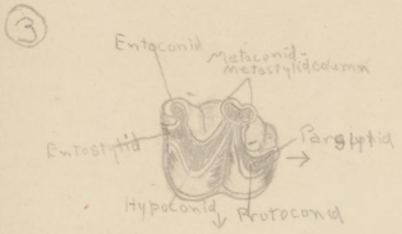


Mesohippus



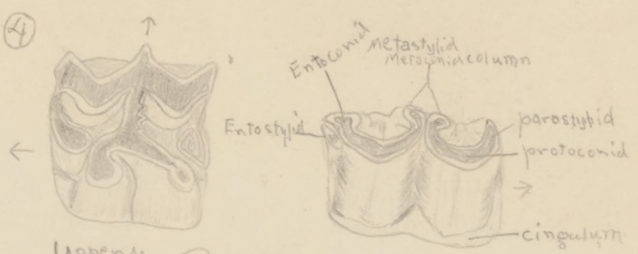
$M\frac{3}{}$ $M\frac{3}{}$

Echippus

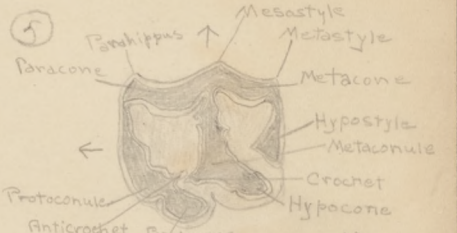


Miohippus

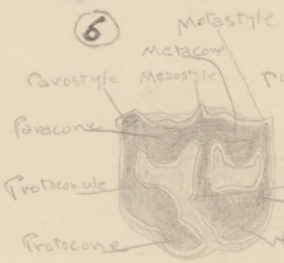
Lower



Parahippus



Primitive Merychippus



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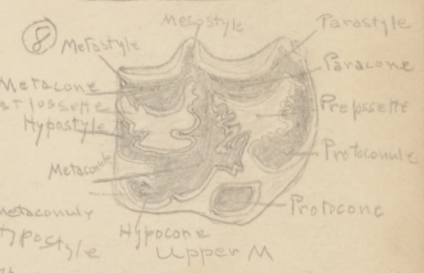
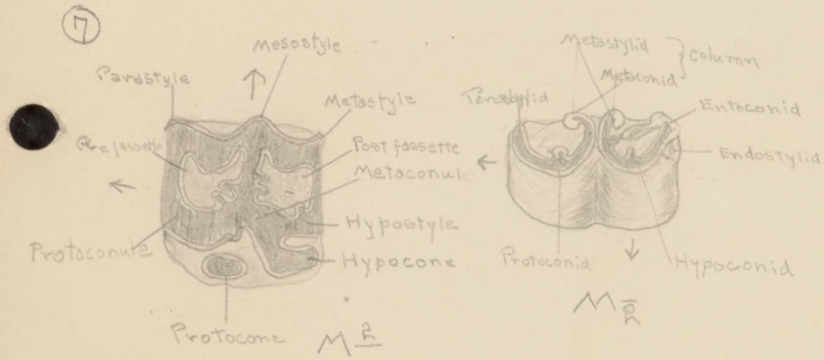
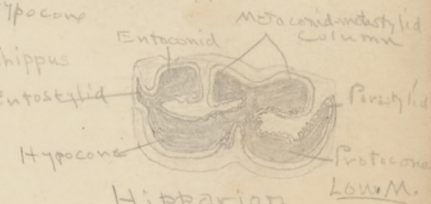
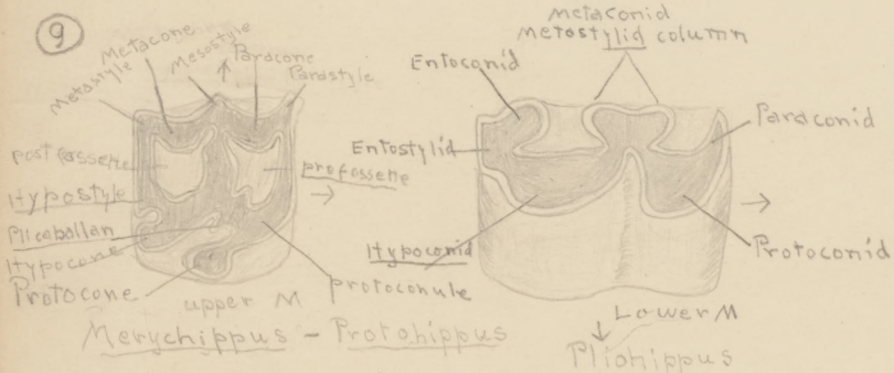




Merychippus isonesus

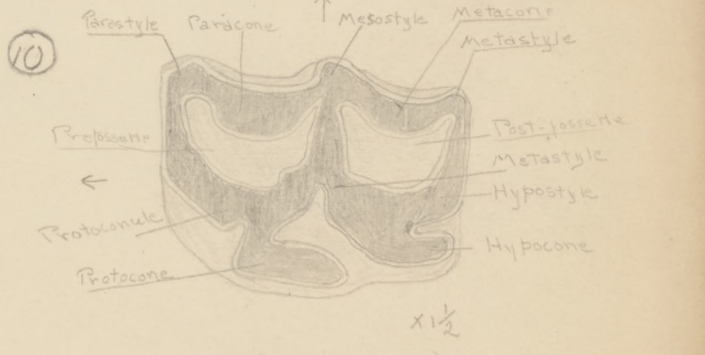


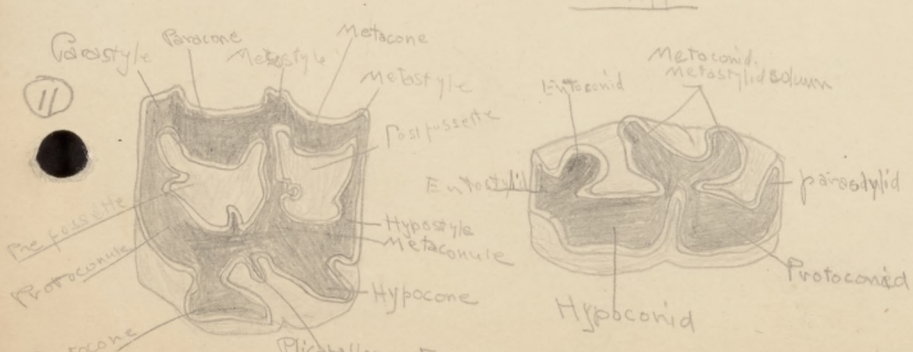
Hipparion



Merychippus - Protohippus

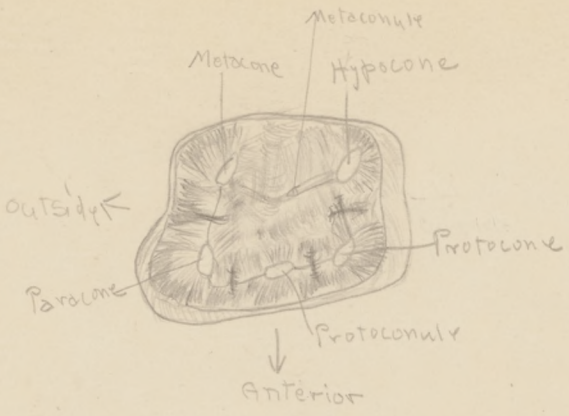
Pliohippus





Pliohippus proversus

H. Howard



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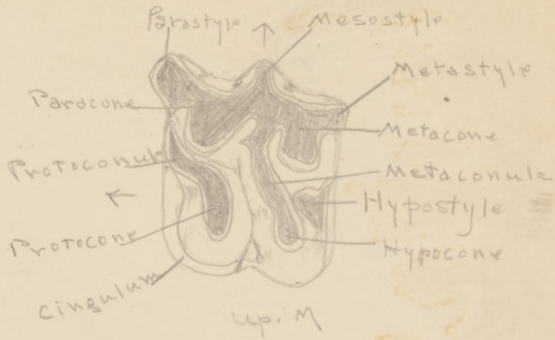

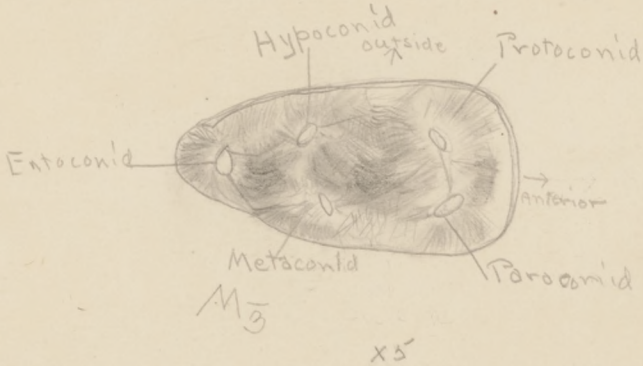

M 3

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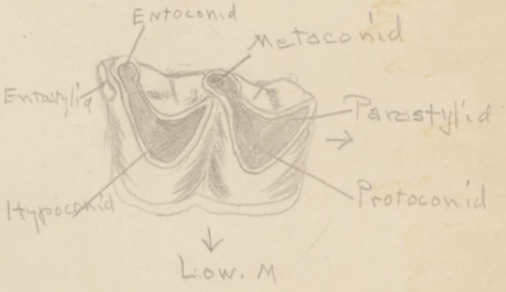
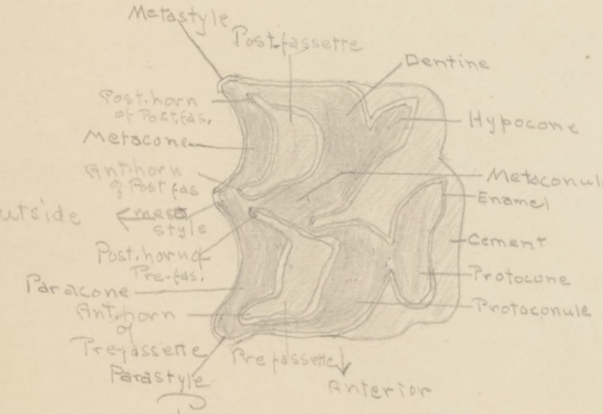


Eohippus

Hypohippus



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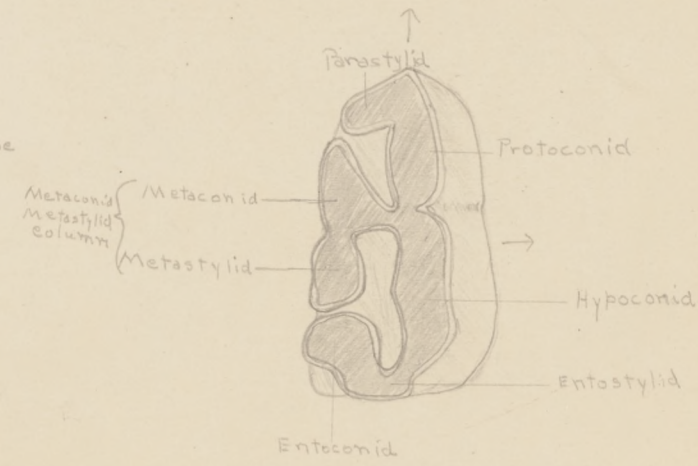


Equus occidentalis

Theories of the Origin of the Vertebrates

(A)

This paper shows very thoughtful work C. L. C.

Geoffrey St. Hilaire
Insect theory
A vertebrate is an insect turned on its back.
Theory later developed by Patten and combated by Cuvier

1864 -- Leidig
Segmentation theory
Applied Darwin's natural selection and origin of the vertebrates.
The segmentation of the Arthropoda and Annelida is homologous with the metamerism of the vertebrate body.

1866 -- Kovaleskyn also Haeckel and more recently Brooks
Appendicularian theory
The appendicularia larva of the Ascidian represents the least modified type of chordate with notochord and dorsal nerve cord.
The adult is sessile, the larva free swimming, and the indications point to it being a form which is giving up its sessile habits

1875 -- Dhorn and Semper
Annelid theory
The mesonephric tubules of the shark embryo are like the annelid in having flame cells.
Dhorn endeavored to describe the hypothetical form connecting the annelids and the vertebrates.
The annelids have a ring of nerve tissue around the oesophagus.
The vertebrate mouth is thought of as a new structure formed by the coalescence of some of the gill slits.
The 4th ventricle is thot to be placed where the gut pierced the brain in chordate ancestors.

1877 -- Lankester, 1883 -- Hubrecht, 1909-1913 -- Chalmers-Mitchell.
Nemertinean theory
The nemertine worm is taken as the nearest relative to the chordates.
The proboscies is thot to change to the notochord.
The mouth gives rise to the vertebrate hypophysis.
Paired longitudinal blood canals form the vertebrate vascular system.
A migration of the lteral nerve cords forms the dorsal nerve system of vertebrates.

1886 -- Bateson
Balanoglossus, or Echinoderm theory
Balanoglossus is a chordate, tho it resembles a worm.
In one stage it is bilaterally symetrical and similar to the Echinoderm larva -- covered with ciliated glands.
Such a form as an ancestor is thot to have given rise to the radiate animals on one hand and the bilaterally symmetrical vertebrates on the other.

1889 -- Gaskell
Limulus- ammocoete theory
The cavity of the gut of Limulus is thot to have become the cavity of the brain of the vertebrates
The space between the paired appendages is homologous with the lumen of the vertebrate gut.
A complicated change of function of nerves and alimentary system is involved.
The vertebrate digestive tract develops from tissue surrounding the gills.

1888-1912 -- Patten 4

Arachnid theory

The ancestors of the vertebrates are thot to be the Merostomata -- a Limulus-like form of the Devonian.

Metamerism of vertebrates is homologous with that of arthropods.

The brain is also homologous

Cephalic pocket on the lower side of the head of Limulus gives rise to the new mouth of vertebrates.

The cerebellum and medulla arise from the invertebrate ventral ganglion (Suboesophageal), the other parts from dorsal ganglion

The cranial flexure of the vertebrates is represented by the original position of dorsal and ventral ganglia. The change is due to the concrescence of the nervous system -- a fusion of segments.

The difficulty here involved is that the invertebrate eye must be turned inside out and upside down and has to migrate to the dorsal surface to be homologous with the vertebrate eye.

1899 -- Willey, Arthur

Amphioxus, or Protochordate theory

This theory does not favor the idea of the protochordate being degenerate

The echinoderms are originally ancestral

1884 -- Adam Sedgewick

Rejects all ideas of the vertebrates arising from highly organized groups, and goes back to the Coelenterates

The mesoderm of vertebrates, according to this theory must be independently developed.

Blastopore = Coelenterate mouth, from which both the mouth and anus are derived

The medusae are the ancestors

1909 -- Goodrich

Rejects all early theories

Believes the chordates were established as soft-bodied animals as far back as Cambrian times.

The idea that the vertebrates did not originate from a highly specialized group, but that both the highly specialized invertebrates and the vertebrates had a common origin as far back in evolution perhaps as the Coelenterates seem to be the most feasible theory yet advanced.

Two lines of evolution of invertebrates — the Tiloblastic + Enteroblastic series — latter includes Amphioxus, Tunicates, Prosomyzia and Echinoderms + the Vertebrates.

Evolution of the Skeleton

Axial Skeleton

The skull and vertebral column surround and protect the brain and spinal cord. Thus the skull may be said to be an enlarged, specialized portion of a continuous axis, tho Oken's idea of the skull being a complex of three or four vertebrae is no longer held. The skull differs from the vertebral column in having many membrane bones.

The foundation around which the vertebrae and posterior part of the skull are developed is the notochord. This is primitively an entodermal, unsegmented rod, extending from the infundibulum to the posterior end of the body. The stages in the evolution of vertebrae are shown in Plate VII, and a brief description of each figure as given in Wiedersheim will suffice.

Fig. 1. A primary sheath is secreted by the peripheral notochordal cells, and a skeletogenous layer is developed from the surrounding mesoderm.

Fig. 2. The central cells of the notochord become vacuolated and the peripheral cells give rise to a secondary sheath. Paired dorsal and ventral cartilages arise in the skeletogenous layer. Cyclostomes, Cartilaginous ganoids.

Fig. 3. The cartilage cells having passed thru the primary sheath, are invading the secondary sheath. Elasmobranchs, Dipnoi.

Fig. 4. The cartilages grow around the notochord, outside the sheaths, and the sheaths become reduced. Bony ganoids, Teleosts, Amphibia, Amniota.

Fig. 5. A precaudal vertebra at a later stage. The notochord is constricted, and the cartilages are united into a single mass, giving rise to a centrum, neural arch, neural spine, transverse processes, and articular processes. Mammals.

With the appearance of cartilage, segmentation is introduced, caused, primarily, by the musculature. The column becoming unbendable, divisions into blocks occur to allow for movement of the trunk, the blocks alternating with the myotomes. Before the evolution of a single centrum, as is present in the mammals, there may be one or two stages in which there are two or three centra more or less fitted in together. Such conditions are represented in the amphibians as shown in Plate VII B. Similar conditions of intercentra and pleuracentra occur in the reptiles.

The calcification of the cartilage may occur in three ways as shown in Plate VII, Fig. 6, 7, 8). Calcification begins to take place in the Bony Ganoids and Teleosts.

Fig. 6. Cyclospondylous. Calcification takes form of double cone, constricted in the middle.

Fig. 7. Tectospondylous, Concentric layers may be added to the above type.

Fig. 8. Asterospondylous. Longitudinal plates formed radiating outwards from the double cone.

Embryonic in Amphibia + Amniota

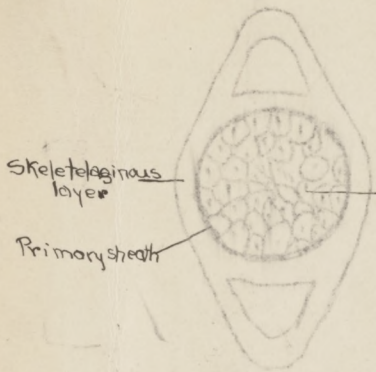


Fig 1.

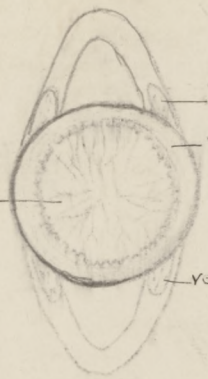


Fig. 2

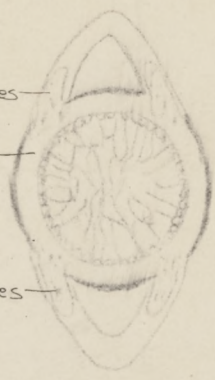


Fig. 3

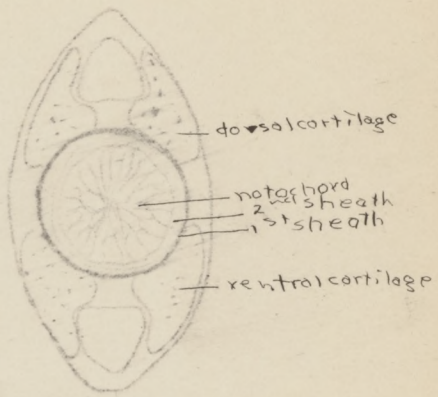


Fig 4.

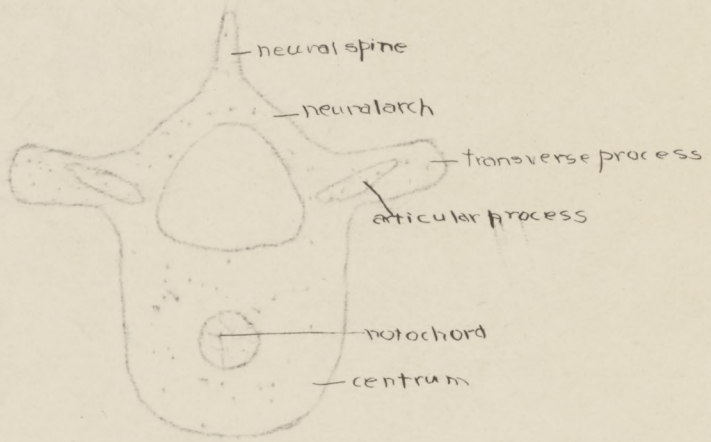


Fig. 5.

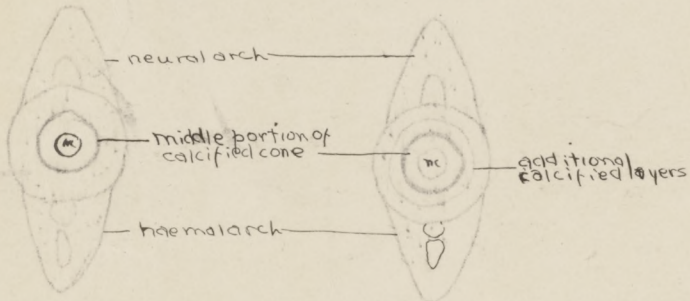


Fig. 6

Fig. 7

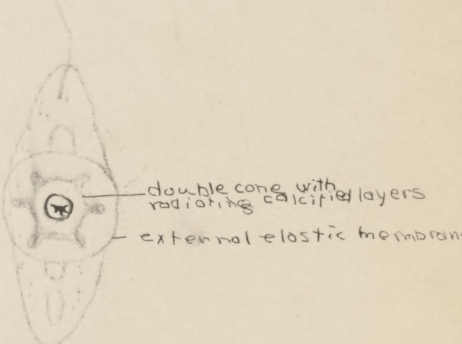
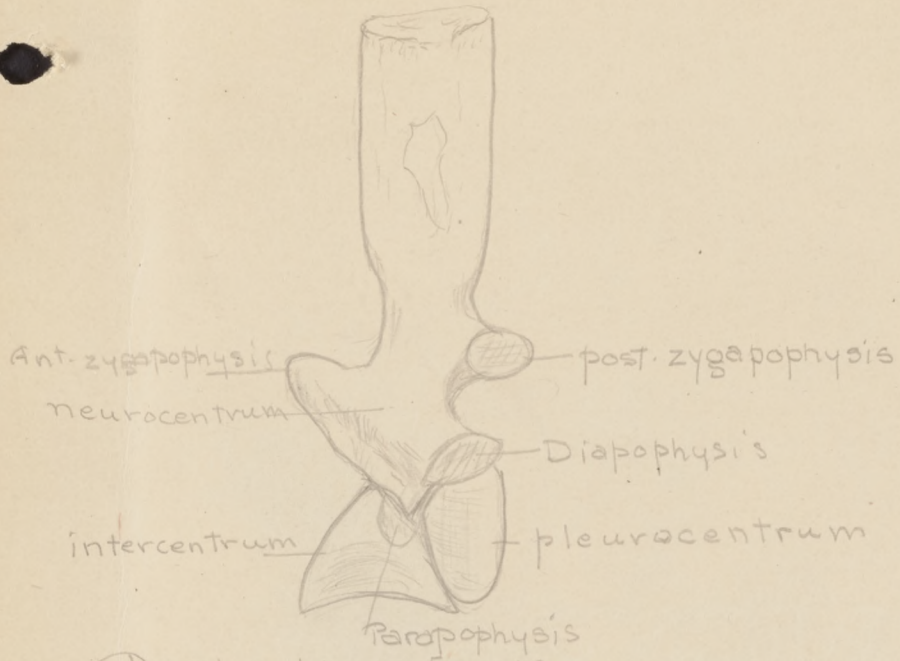
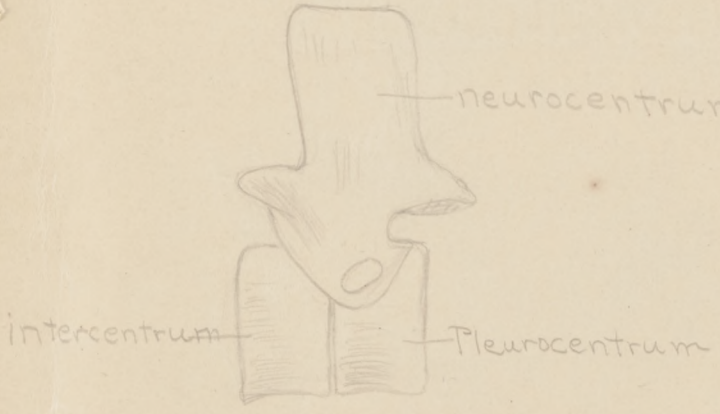


Fig. 8



Rachitomous

Dorsal vertebra of Eryops



Embolomerous

Dorsal vertebra of Cricotus

Stereospondylous -

Dorsal vertebrae of Crossotelos

Evolution of the Skull

The simplest type of vertebrate skull is a membranous skull, in the substance of which is formed the cartilaginous chondrocranium of adult Elasmobranchs and of the young of all other higher vertebrates.

The chondrocranium is developed as follows:

The parachordal plates are the first to develop, arising vexntrally on either side of the notochord, which extends forward under the brain to the infundibulum. The parachordal plates extend laterally to the ears, anteriorly to the end of the notochord, and posteriorly to the exit of the tenth nerve. Following the development of the parachordal plates, an otic capsule is formed around each internal ear, joining the paracnordals and forming a trough in which lies the posterior part of the brain. The floor of this trough is made up of the notochord with the parachordal plates which together are known as the basilar plate; the sense capsules form the sides. Anteriorly a similar trough is formed consisting of two cartilages extending forward from the posterior part. One pair -- a lower pair -- the trabeculae cranii, join the anterior margin of the basilar plate. Another pair -- dorsal -- the alisphenoid cartilages, become connected finally with the anterior wall of the otic capsules. The anterior floor of this trough is formed by the anterior union of the trabeculae in an ethmoid plate, the posterior part, in lower vertebrates is membranous.

The above is in part the condition of the skull in the Cyclostomes. (See figs. 1 and 2). Other elements, however, are present, which cannot be directly traced thruout the higher forms. Such elements are the anterior cartilages -- anterior lateral, anterior dorsal and annular -- the latter supporting the mouth; the large lingual cartilages, supporting the tongue and thought by some to represent the labials of higher forms; and the subocular arch, possibly a representative of the pterygquadrate, tho the homology here is questioned.

The Myxinoid skull is even more primitive than that of Petromyzon -- both its roof and side walls are membranous and the single cartilage capsule surrounding the nasal tube is in the form of incomplete rings. The Petromyzon skull is also partly membranous, tho possessing a dorsal bridge between the auditory capsules.

The Elasmobranch skull is far in advance of the Cyclostome, and, unlike the Cyclostome, the elements may be readily correlated with those of the higher forms. The skull is a true cartilaginous chondrocranium. Parachordals, otic capsules, alisphenoids, trabeculae and ethmoid plate are present, and the trabeculae are not united until reaching the ethmoid, leaving the floor of the cranium open. This is the platybasic condition of the skull and is correlated with the anterior extension of the brain.

In addition to the elements already mentioned the Elasmobranch chondrocranium has a pair of nasal capsules around the olfactory organs, and united to the cornua, alisphenoids and ethmoid plate. The eyes are also surrounded by sense capsules which in order to allow for the movement of the eye, never unite with the rest of the cranium. Posterior to the otic capsules are three or four occipital vertebrae, alternating with the myotomes, like vertebrae.

So far as can be ascertained, the Elasmobranchs are the first vertebrates to possess jaws, unless the toothed edged dermal plates in front of the mouth in the Antiarchi (Ostracoderms) be considered true jaws. The jaws in the Elasmobranchs are formed from the first gill arch, the mandibular -- the lower composed of Meckel's cartilage, the up-

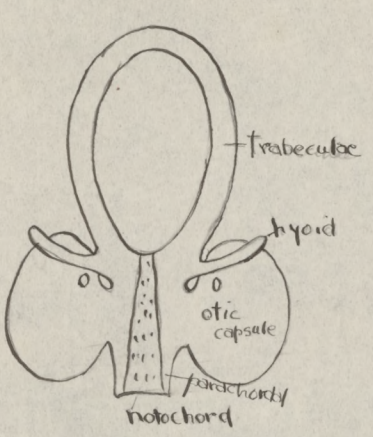


Fig. 1 Chondrocranium of Ammocoete stage of Petromyzon

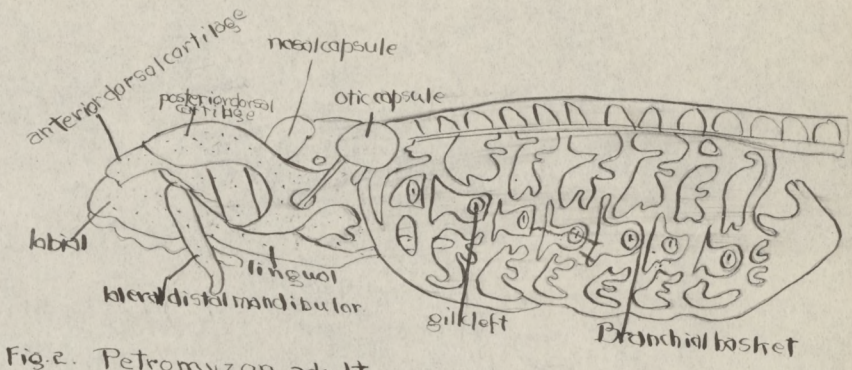


Fig. 2. Petromyzon adult

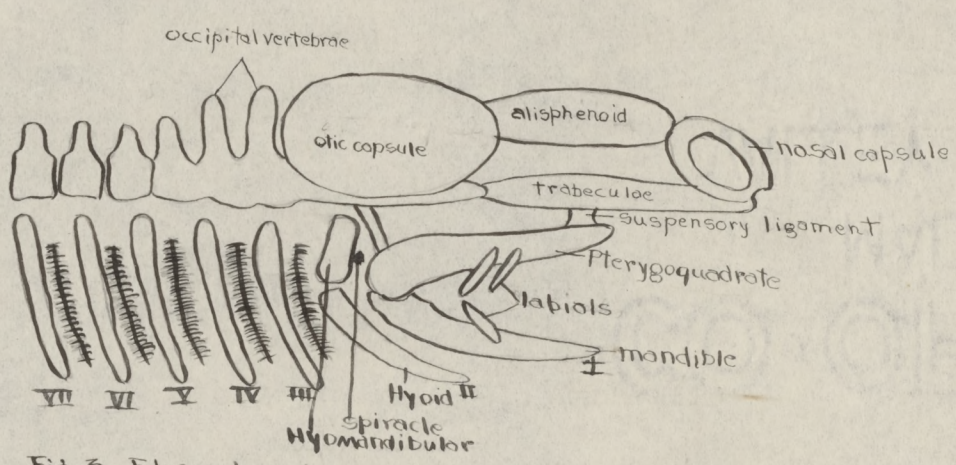


Fig. 3 Elasmobranch

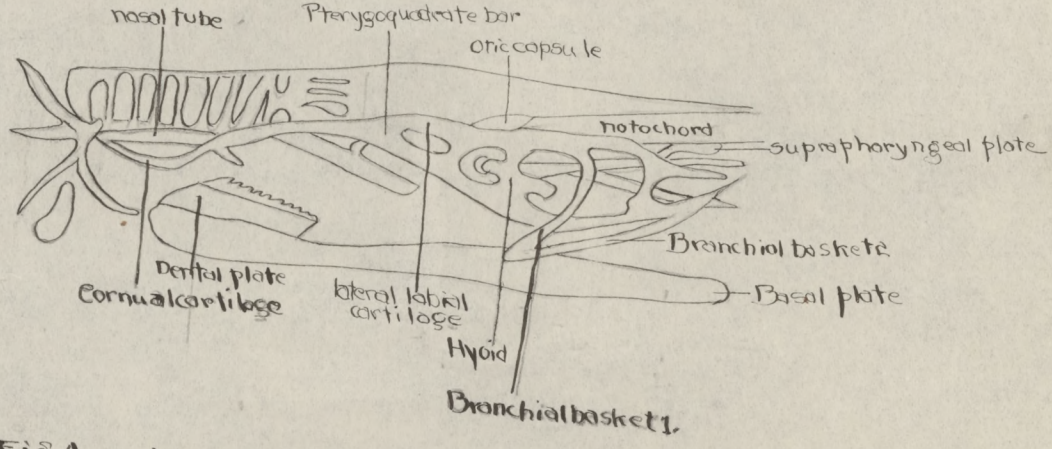


Fig. 4 Myxinoid

per of the pterygoquadrate. In the majority of Elasmobranchs, the skull is hyostyllic -- the pterygoid being supported anteriorly by a pair of ethmo-palatine ligaments and posteriorly by a ligament and the hyomandibular arch. However, there are several variations of this condition more or less interlocking. In the Cestracionts, the pterygoid is suspended by the hyomandibular posteriorly, but anteriorly it articulates with the cranium. Among the Notidanids, a true amphistyllic condition is found, wherein the pterygoquadrate articulates directly with the post-orbital process of the cranium, the hyomandibular no longer acting as a posterior suspensor, but being connected with the rest of the hyoid. The Holocephalans have a hyostyllic condition in the young, but the adult is autostyllic -- the upper jaw being fused to the cranium, as in the higher forms. (Fig. 3 for Elasmobranch skull).

Above the Elasmobranchs, the cartilaginous chondrocranium shows certain centers of ossification, giving rise to the so-called cartilage or replacing bones. These may be classed in four groups: the occipitalia, the sphenoidalia, and ethmoidalia, there being two sets of sphenoidalia.

The occipitalia arise in the occipital vertebrae and in the basilar plate, and are four in number, forming a ring around the foramen magnum. The four are: supraoccipital, two exoccipitals, and a basioccipital.

In front of the basioccipital, the basilar plate ossifies to form the basisphenoid, extending forward to the sella turcica, from whence it is succeeded by the presphenoid, which arises from the trabeculae and extends forward to the ethmoid. The alisphenoid cartilages ossify into the bones by that name and also, more anteriorly, into the orbitosphenoids.

The ethmoid plate ossifies into a median mesethmoid bone, having on either side of it an ectethmoid.

In the otic capsules the petrosal bones develop, consisting of a prootic, in front, an opisthotic, behind, and between them an epiotic. There may be in addition in the teleosts a sphenotic (anterior) and a pterotic (posterior) forming in the lateral of the otic capsule. As we will see, the otics later fuse to form a single petrosal bone.

The nasal capsules may develop a lateral ethmoid on the upper wall, and ethmoturbinals on the medial and lateral walls.

Beside the ossification of the cartilage elements, the skull of vertebrates above the Elasmobranchs is provided with a number of membrane bones, first present in the ganoid fishes as scales. Nearly all of the dermal scales of the ganoids may be homologized with the membrane bones of the teleosts, if we consider that one bone in the teleost may represent a fusion of two or three which are present in the ganoid.

On either side of the median line on the dorsal side of the skull are: a pair of nasals, in the olfactory region; a pair of frontals, between the orbits; a pair of parietals on a level with the otic capsules; an interparietal, arising from paired centers, between the parietals and the supraoccipital. This in the higher groups is fused with the supraoccipital. In the lower groups there are other membrane bones developed: a supratemporal, lateral to each parietal; a postfrontal, articulating with the frontal behind the orbit; a postorbital, lateral to the postfrontal. There may also be supraorbital bones on the medial

wall of the orbit. A prefrontal may bound the orbit anteriorly, and lateral to this there is usually a lacrymal. An intertemporal bone is found in certain of the reptiles. A tabulare is present in fishes, amphibians and some reptiles; it lies above each otic capsule. A parasphenoid is present in some amphibians and reptiles where the basilar plate and trabeculae fail to ossify, and form the floor of the cranium. Vomers are present also just anterior to the parasphenoid. The vomers of the vertebrates below the mammals are often called prevomers, and the parasphenoid is thought to represent the mammalian vomer.

Other bones are added to the skull from the mandibular arch. The median portion of the pterygoquadrate disappears, and as the remainder of the bone becomes more closely connected with the cranium anteriorly, is replacedby a pair of membrane bones, the palatines, lying between the parasphenoid and the vomers. The rest of the pterygoquadrate then ossifies as two bones on either side, a pterygoid, anterior and a quadrate, posterior. In the teleosts and the reptiles the pterygoids are composed of a series of bones. Outside the pterygoquadrate an arch of membrane bones develops, taking over the function as upper jaws. These bones are: a squamosal, overlying the quadrate; a quadratojugal, anterior to the squamosal; a jugal, a maxillary and at the tip of the jaw, a premaxillary which articulates with its fellow of the opposite side.

The roof of the skull of the lower vertebrates is continuous, having only openings for the nares and orbits. Certain fenestrae appear in the higher groups, as will be described below in the reptiles.

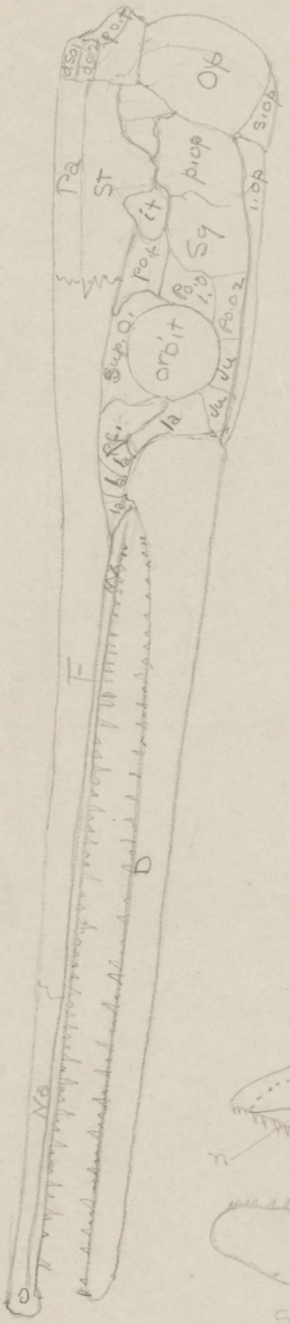
The above is a general summary of what occurs in the evolution of the skull. It remains now to give briefly the groups in which the different changes take place.

In the class Pisces, there is a development of skeletal supports for the opercular fold, which covers the external gill apertures. These supports, the opercular bones, are dermal in origin and include the preoperculum, operculare, suboperculum, and interoperculum. The opercular bones are peculiar to the fishes, dropping out ~~again~~ in the amphibians. The other bones of the fish skull, however, with few modifications, persist thruout the vertebrate evolution. These bones are as follows: (Plate II, Figs. 1, 2, 3, 4)

Cartilage bones
- Occipitals
  - Supraoccipital
  - Exoccipitals
  - Basioccipital
- Sphenoids
  - Basisphenoid
  - Alisphenoids
  - Orbitosphenoids
- Ethmoid
- Otics
  - Opisthotic
  - Prootic
  - Epiotic
  - Sphenotic
  - Pterotic
- Pterygoids -- Entopterygoid, Mesopterygoid, Metapterygoid
- Quadrate

Plate 2

Dorsal view of skull
Lepidosteus
Fig 1



lateral view
Fig. 2

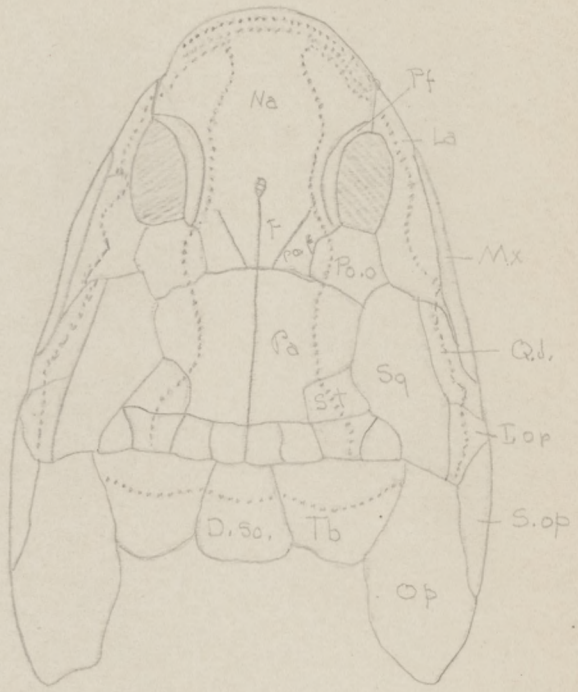
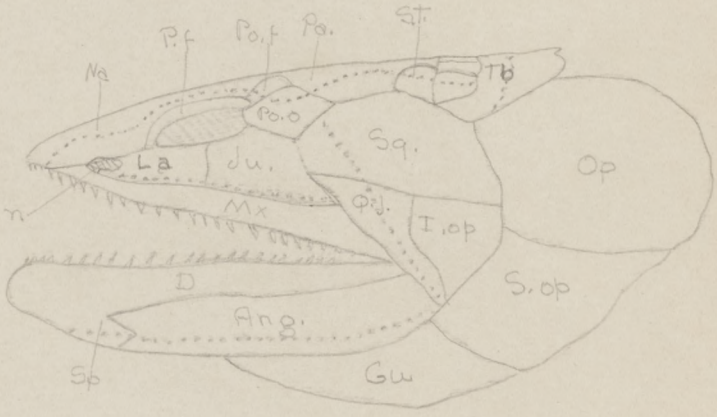


Fig 3 Dorsal view



lateral Fig 4
Osteolepis

Na – naso-ethmoid
F – frontal
Po.f – postfrontals
Pa. – parietals
Pf. – prefrontals
La. – lacrymal
Ju. – jugal
Po.o. – postorbital
S.t. – supratemporal
Sq. – squamosal
Mx. – maxilla
Q.J. – quadratojugal
D. – dentary
Sp. – splenial
Ang. – angulare
Op. – operculum
S.op. – subopercular
Gu. – gular
I.op. – interopercular
D.So. – dermosupraoccipital
Tb. – tabular
P.op – preoperculum
IT – intertemporal

Membrane bones
- Frontals
  - Frontal
  - Prefrontal
  - Postfrontal
- Nasals
- Parietals
- Parasphenoid
- Vomer
- Premaxillary
- Maxillary
- Jugal
- Squamosal
- Lachrimal (Lackrymal)
- Quadratojugal
- Supratemporal
- Orbitals
  - Pre-orbital
  - Postorbital
- Opercular bones
- Tabulare

We may say that the fishes represent the first true skull development; having in the ganoids the conversion of dermal scales into dermal elements functioning as bones, and in the teleosts, in addition to the dermal elements, a practically complete replacement of the cartilage giving rise to the cartilage bones named above. The jump from the cyclostome type of skull to the fish type is a large one, but beyond the fish, there is a gradual evolution which may readily be traced from one class to the next. In each class there are the more primitive members which largely resemble the more advanced members of the preceding class.

As noted before, the first modification of the fish skull is the dropping out of the opercular bones. The quadrate becomes permanently united to the skull and in the Amphibians is made up of four parts, the basal, otic, ascending, and pterygoid; the otic and ascending processes uniting with the cranium. An important modification occurring in the amphibians is the first development of an inner ear bone. An opening occurs in the otic cartilage, or periotic bone, known as the fenestra vestibulae. The fenestra is covered by a stapedial plate which is connected with the quadrate by a handle like protruberance, the columella. This subject will be taken up in more detail in a treatment of the development of the ear bones. It is sufficient tosay here that probably this stapedial plate and columella are represented in the fishes by the hyomandibular which is otherwise missing in the amphibians. (See Plate II, figs. 1, 2, and 3 for Amphibian skull).

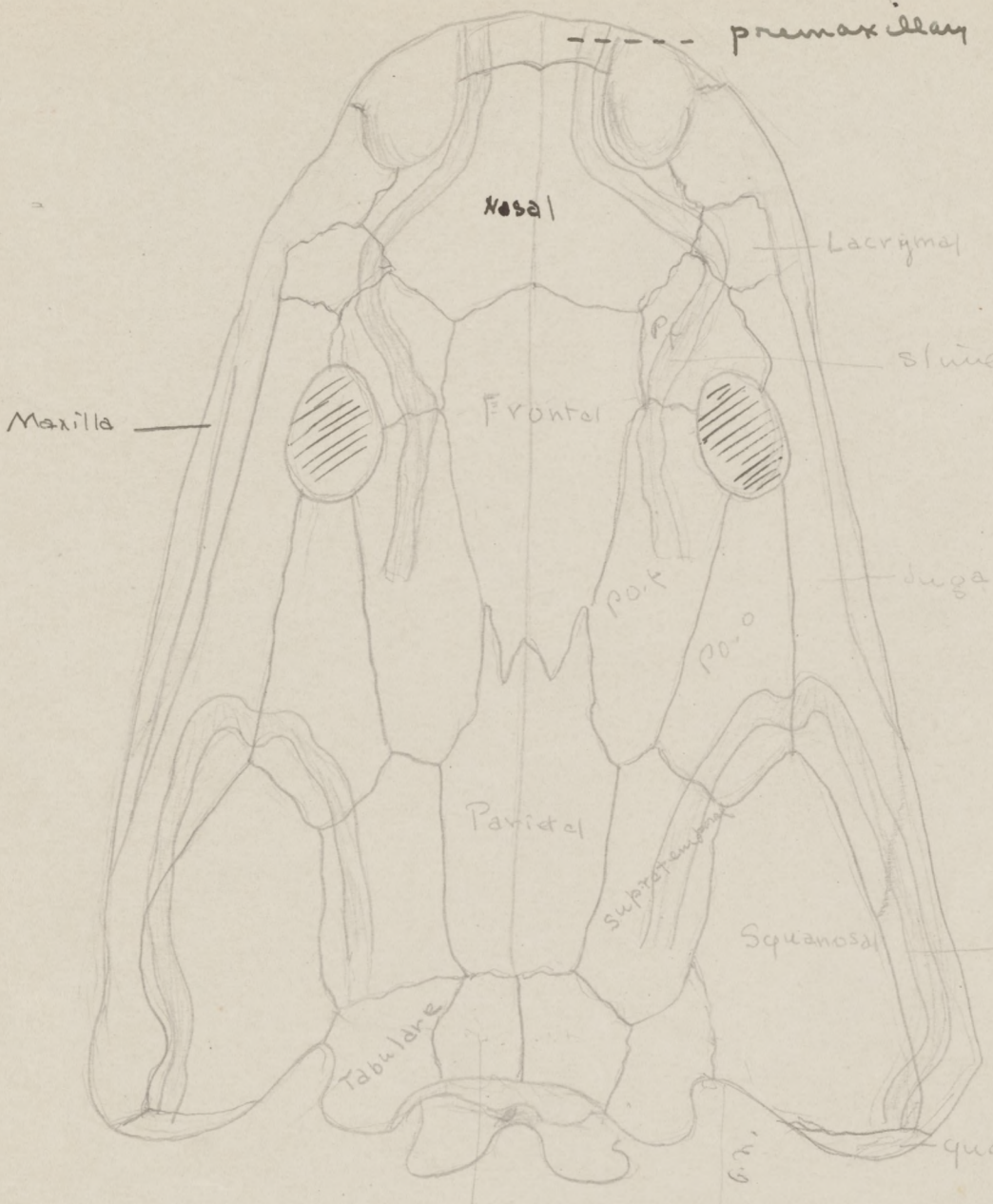
The membrane bones which in the fishes were in close connection with the skin, separate from the integument and sink to a deeper position. This condition may be noted in modern amphibians, tho the primitive amphibians showed indication of the associatin of the skin and bone.

With further development the bones of the skull become harder and more easily preserved, so that fossil remains of vertebrates higher than the amphibians seem to be more plentiful. With this condition, in the reptiles, comes the enlargin of the temporal region by the outgrowth of bars, surrounding spaces in the skull in which there is no brain. These spaces are known as fenestra. In the more primitive reptiles no fenestra are present, tho in these there is an additional

Plate 3

Amphibian
Stegocephalians
Stereospondylous

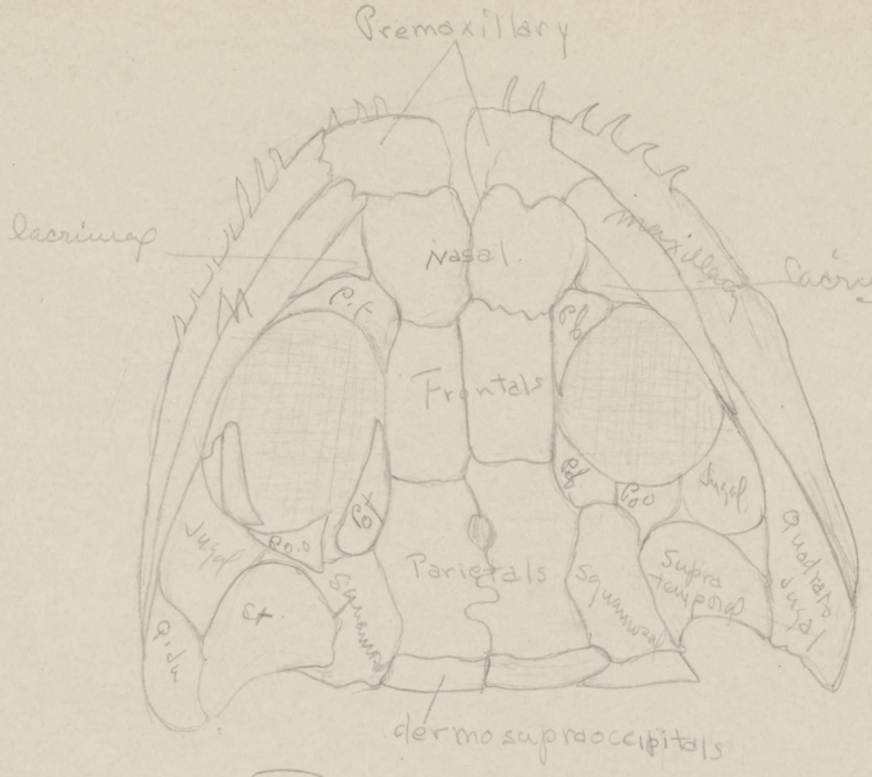
Plate III



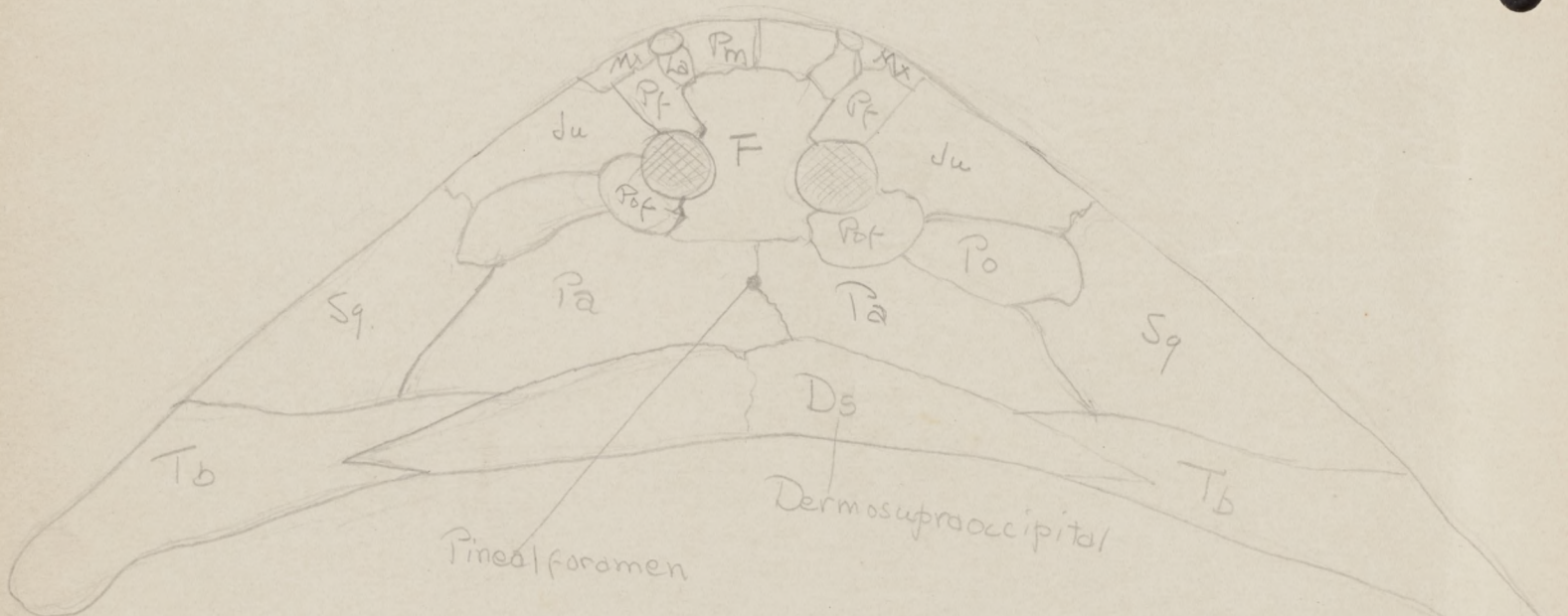
Metopias diagnosticus

Fig. 1.

Plate III



Branchiosaurus Fig 2



Diplocaulus Fig. 3

bone in the temporal region, the infratemporal, not present in amphibians. (Plate IV, Fig. 1a). The modern turtle is a living representative of the primitive type of skull which lacks fenestration (Plate IV Fig. 2a, 2b, 2c).

One fenestra occurs in the Synapsid reptiles, lateral in position (Plate IV, Fig. 4a, 4b). Two fenestra are present in the Diapsida, a lateral fenestra, homologous to that of the Synapsida, and a dorsal. A further modification of this type is found in the Dinosaurs which have, in addition an anterior fenestra. (Plate IV, Figs. 3a dnd 3b, and (Plate XII Fig. 1). Two fenestra are also present in the Parapsida, a dorsal, and a lateral which lacks the lower margin present in the Diapsida. It is thought that this type of skull is derived from the Anapsid and Synapsid group and is of separate origin from the Diapsida. (Plate IV Fig. 5a, 5b).

The bones of the skull of reptiles are practically similar to those of amphibians as may be seen from the accompanying diagrams. There are, however, some fusions in the cartilage bones, while at the same time membrane bones and processes are added. However, as the Amphibians do not lie in the direct line of descent of the Reptiles, these differences are natural. A list of the membrane bones of reptiles follows:

Parietal -- often a fusion
Frontal -- " " "
Nasal -- " " "
Squamosal
Prefrontal
Septomaxillary
Postorbital
Jugal
Quadratojugal
Lacrymal
Paraquadrate
Parasphenoid
Premaxilla,
Maxilla
Vomer
Palatine
Pterygoid
Transpalatine

Among the Sauropsida, a further development of the stapes takes place, taking on the well known stirrup-like form.

Evolution of Lower Jaw

The essential feature in the evolution of the lower jaw is the loss or fusion of many of the bones present in the lower vertebrates.

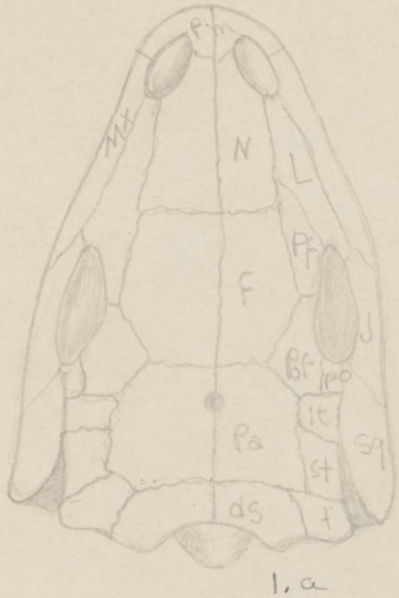
The Fishes have more coronoids than amphibians, amphibians, reptiles one, and mammals none. There is also a loss of one of the splenials in reptiles. Amphibians have a postsplenial and a splenial, reptiles have only a splenial, the mammals have none. A surangular present in reptiles is questionably present in amphibians. All posterior elements of the jaw are lost in mammals except the dentary, which here develops a coronoid process, not in the least homologous with the coronoid of reptiles. (Plate V, Figs. 1,2, 3, 4, 5)

Plate IV

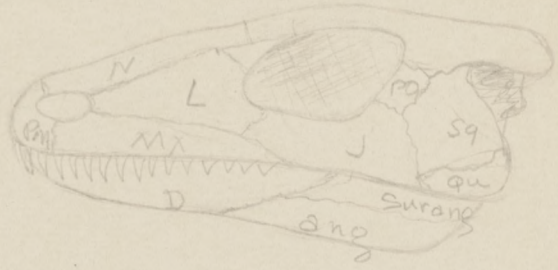
The primitive reptiles

Anapsida

Seymouria

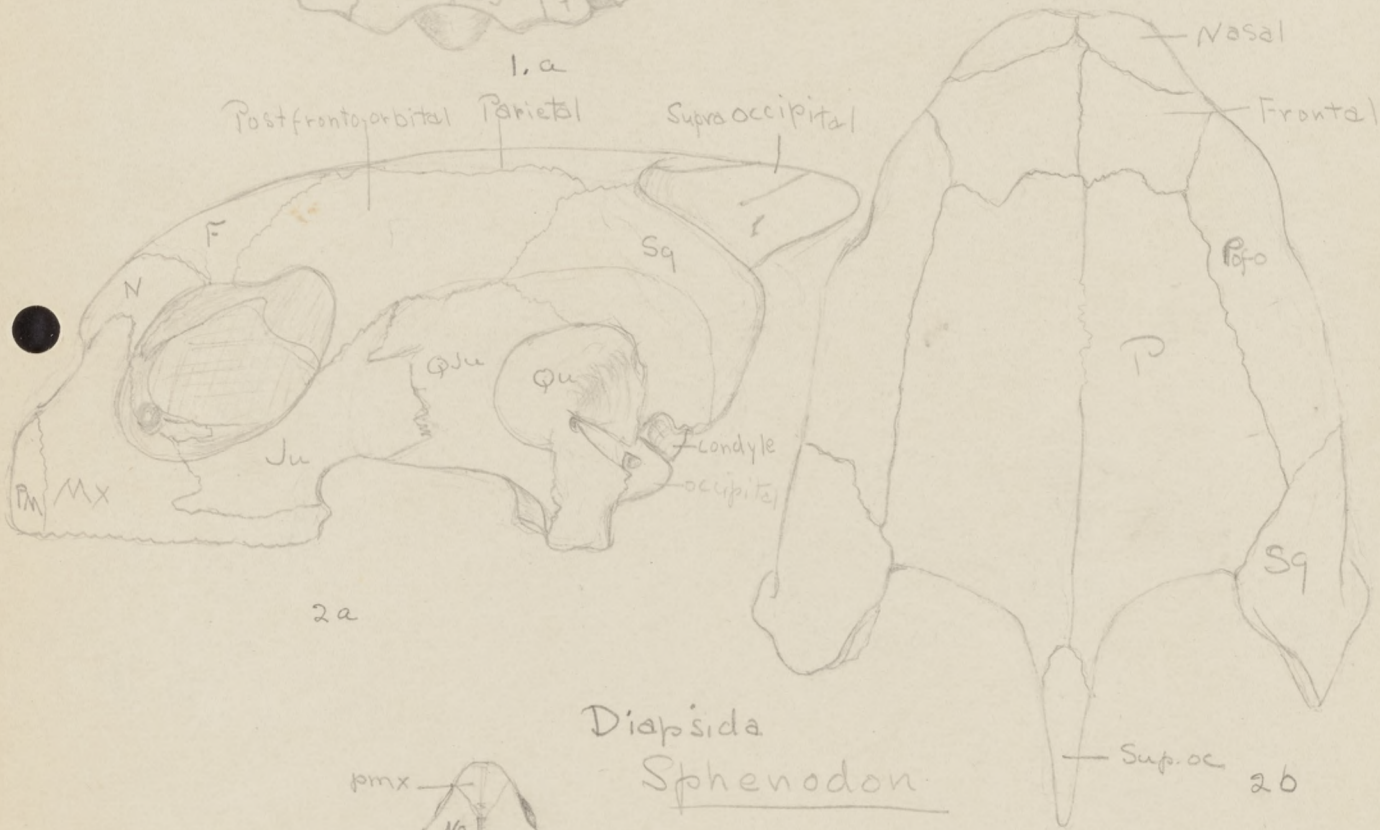


1. a



1 b

Chelonia

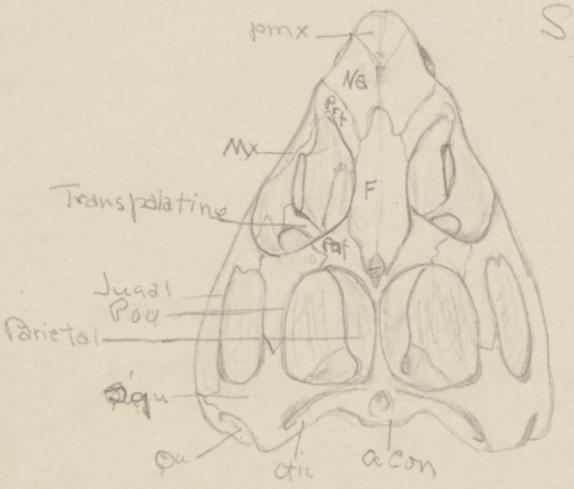


2a

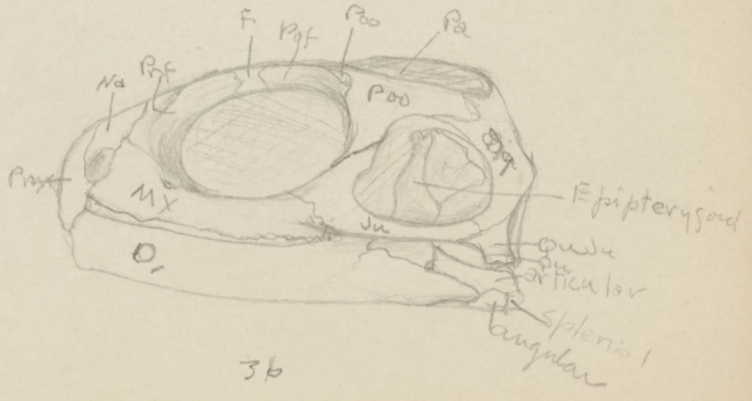
2b

Diapsida

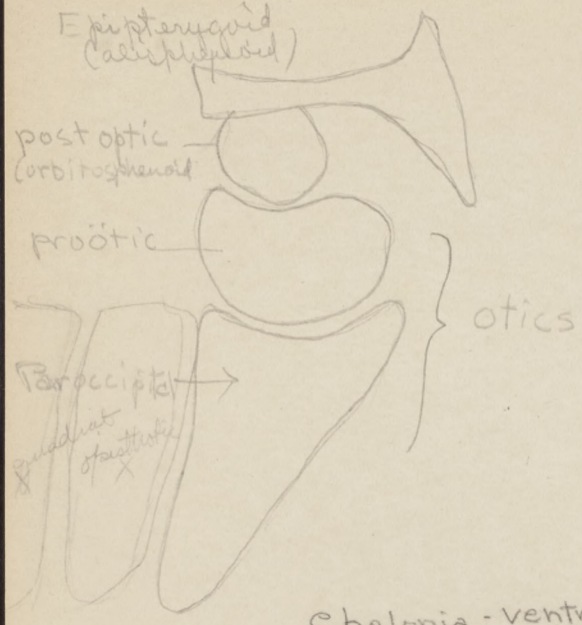
Sphenodon



3a



3b



Chelonia - ventral view

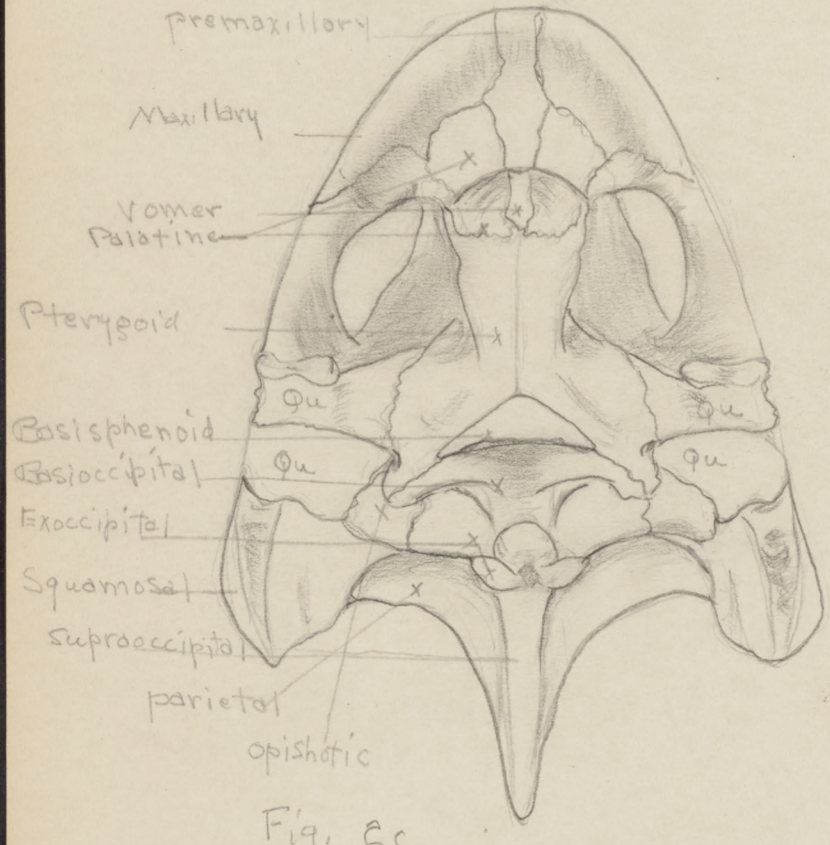


Fig. 2c

Synapsida

Plate IV cont'd

Mycterosaurus longiceps

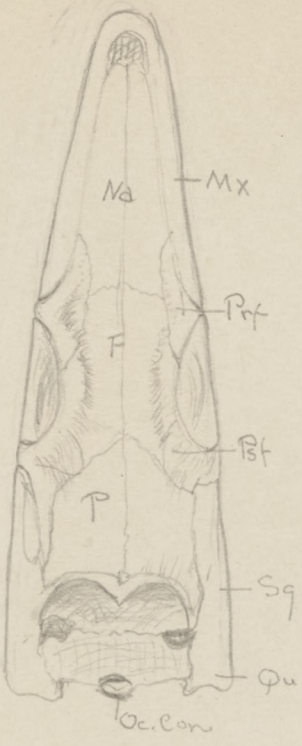
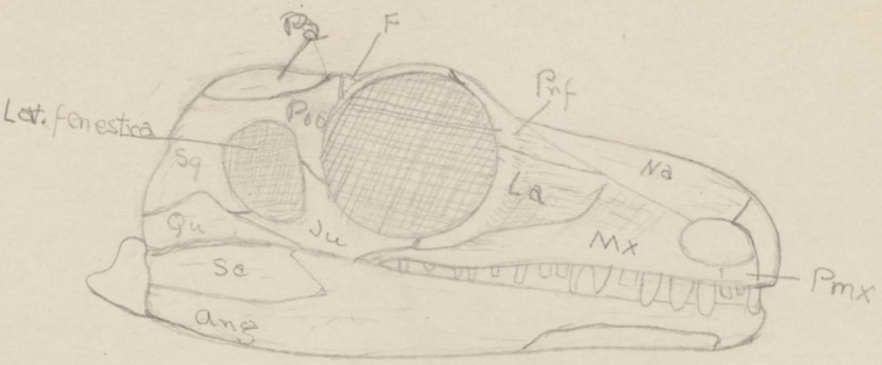
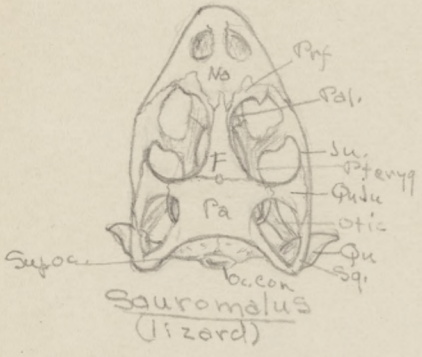


Fig 4 a



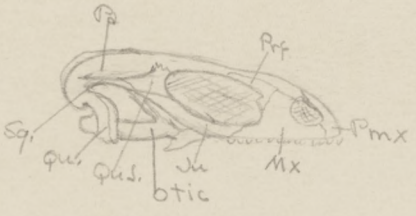
4b

Parapsida



Sauromalus
(lizard)

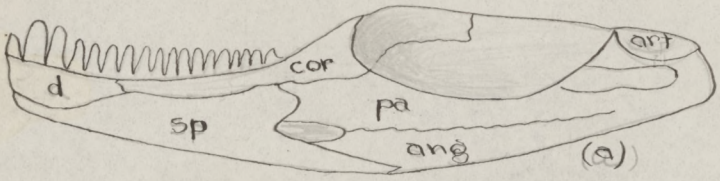
Fig 5a



5b

Plate V

Labidosaurus hamatus



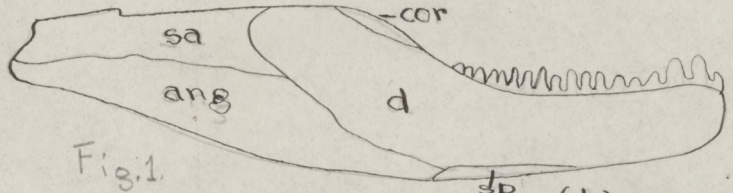


Fig. 1.

Fig.1.

Captorhinus aguti

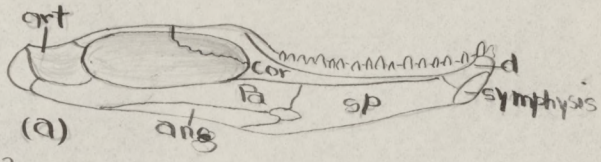
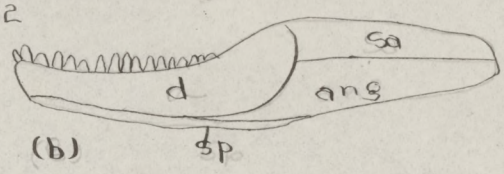


Fig. 2



Trimerorachis alleni

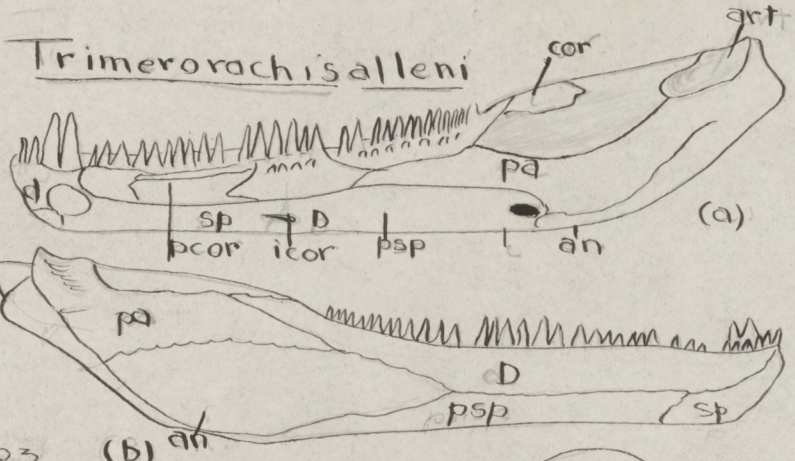


Fig 3

cor = coronoid
D = dentary
sa = surangular
ang = angular
art = articular
pa = prearticular
sp = splenial
psp = posisplenial
icor = intercoronoid
pcor = precoronoid

Diplocaulus

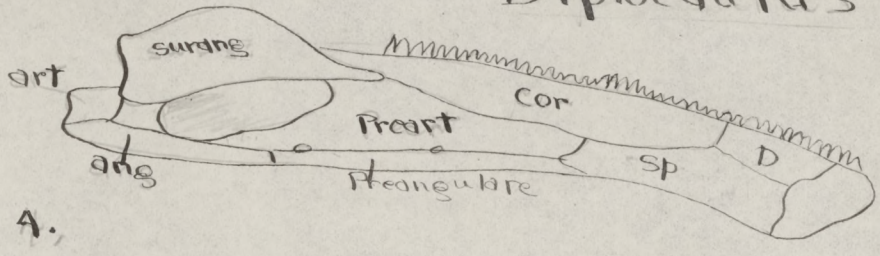
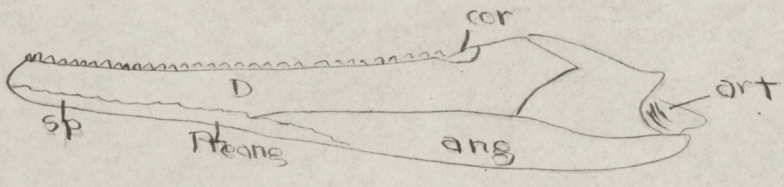
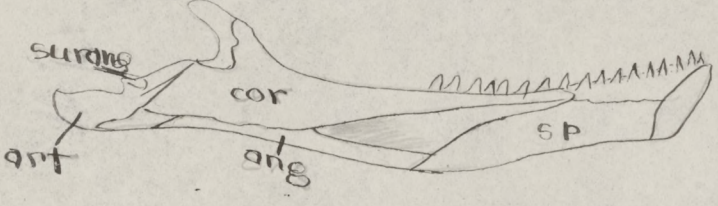


Fig 4.

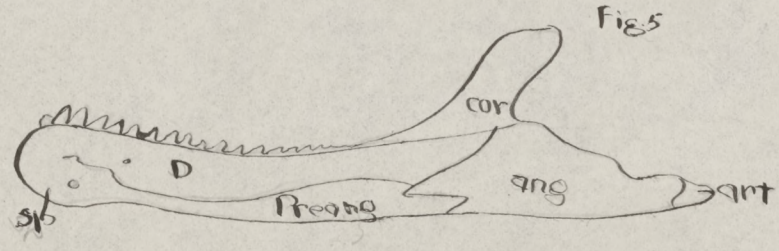


Polypterus



1,2, – reptiles
3,4, – stegocephalian
5, – crossopterygian

Fig.5



Evolution of Dermal Elements

Scales

The epidermis originally covers the scale, which grows out beneath it. The inner surface of the epidermis, in contact with the outgrowing papilla, secretes the enamel and is called the enamel organ. The epidermis is early worn away at the cusp, leaving the enamel covered scale projecting out. The bone-like substance is formed in the dermal layer of the skin by the calcification of the outer layers of the tip and base of the dermal papilla, leaving a vascular cavity within. (Plate VII)

In the shark, placoid scales are present, formed as just described. These scales are very small and stud the surface of the skin, often with no metameral arrangement. There may be fusion of contiguous denticles (scales) as in the case of the enlarged, blunt denticles. Such fusion within the shark group may be a forerunner of what occurs in higher forms -- the ganoids.

In the ganoids the dermal plates, or ganoid scales are thought to have been formed by the concrescence of groups or placoid scales. Accompanying this grouping of denticles, there is a lessening in the importance of the enamel layer, which in the shark was seen to be epidermal. In the ganoid, this surface layer of ganoine is probably of dermal origin, derived from the dentine substance. This fusion of placoid scales to form the dermal, ganoid scales is thought to give rise to the membrane bones of other forms of vertebrates, by the gradual extension of the exoskeleton from the surface to deeper parts.

In the teleosts, the scales are cycloid or ctenoid, the condition being practically the same in both except for modifications. The scales here are overlapping. In some of the ganoids an outgrowth from the scale is known to occur -- overlapping the scale in back of it. It is the development of this outgrowth which has led to the cycloid scale. The original ganoid scale is lessened in size, and importance, becoming known as the "button" in the fishes, which is at the base of the cycloid scale and is overlapped by the scale in front. The enamel and dentine layers are no longer functional and they disappear. The cycloid scale is formed entirely of a calcified tissue developed in the derma -- development occurs in successively deep layers. Therefore, the cycloid scale may be said to represent morphologically the basal region of the denticles of the shark.

Teeth

Teeth are modified scales, of placoid type. Many vertebrates have the power of forming scales in their skin. Therefore with the invagination of the skin to form the stomodaeum, the skin retains this capacity and thus any portion of the stomodeal wall may secrete scale-like plates, or teeth. For this reason they are often found, in some forms, not only on the jaw, but wherever there are skeletal parts to support them: on the vomers, palatine, premaxillary, maxillary, parasphenoid, on the tongue, and the hyoid.

In the fishes teeth are found on the hyoid, in the amphibians, on the vomeropalatine, and parasphenoid, in reptiles on the pterygoid. In all of these forms they may be borne on the maxilla and premaxilla as well. The absence of teeth is a secondary adaptation peculiar to certain groups -- particularly the birds, and turtles, tho in these groups as well, a dental ridge is developed in the embryo.

In the shark there is a continuous formation of new germs and enamel organs for an indefinite period thruout the life of the individual, the epidermis continually coming around in a fold. Such a succession of teeth with slight modifications, occurs in all of the vertebrates, below the mammals. In this latter group there is ~~ax~~ a definite number of germs and enamel organs and tho one enamel organ may continually give rise to a tooth as in the horse, the organ itself is only replaced once, at the time of change from milk to permanent dentition.

The teeth primitively are essentially similar in form (homodont) and this condition prevails thruout most of the vertebrates below the mammals. In the mammals thery become differentiated into incisors, canines, premolars, and molars. ~~(The primitive mammals, however, have more or less undifferentiated teeth)~~ mammal-like reptiles have differentiated teeth.

The teeth of ~~fishes and~~ amphibians are solid, composed of enamel folds and attached at the base of a shallow pocket. This, the labyrinthodont type, is ancestral to the thecodont, or subthecodont teeth of early reptiles.

The thecodont tooth is inserted in a shallow pocket in the jaw, surrounded by the jaw bone.

There are other types of tooth insertion among the reptiles:

Pleurodont -- the teeth being set on the inner edges of the jaws attached by the side and base only.

Acrodont -- where the teeth insert directly on the edges of the mandibles without any pocket.

crossopterygian fishes + stegocephalous

Evolution of the Branchial Arches

The branchial arches of the lampreys of the Cyclostomes, are not true branchial arches which may in any way be homologized with those of fishes. The branchial skeleton, rather, consists of a gill basket of continuous cartilage having fenestrae for the gills, and above and below the gills also. The basket lies immediately beneath the skin and is lateral to the gill pouches and aortic arches. In the myxinoids there are two true gill arches in front of which is a third arch -- possibly the hyoid. (Plate I Fig. 2, 4)

The true branchial or visceral arches number from I to VII. They lie in the septa between the gill clefts and each connects with the other of the pair, below the pharynx to form a copula. Each bar is at first continuous, but later becomes divided. The first two arches become specialized as the mandibular and hyoid arches, the rest lying in the region of the functional gills continue as gill supports. The number of the gill arches varies with the number of gills. (Plate I, Fig. 3)

The Mandibular arch is composed of two parts: the dorsal half, the pterygoquadrate; the ventral half, Meckels cartilage. In the Elasmobranchs and Chondrostei, the pterygoquadrate forms the upper jaw and is joined to the cranium by ligaments. With the appearance of true bone, the pterygoquadrate becomes reduced and ossifies as two or more bones as describedin the evolution of the skull: usually the quadrate and the pterygoid. The fate of the quadrate is given below in the evolution of the ear ossicles.

Meckel's cartilage, in the lower vertebrates, forms the lower jaw. In the higher forms it forms the axis around which the membrane bones of the jaw are arranged. In the mammals the posterior part (articulare) forms the malleus of the ear.

The Hyoid arch is also composed of two parts: the upper, hyomandibular; the ventral, hyoid proper. In lower elasmobranchs, the hyomandibular and the rest of the hyoid, are closely connected. In higher fishes, the hyomandibular separates from the hyoid and tends to intervene between the mandibular arch and the cranium as a suspensor of the jaws. Later it loses its suspensorial function, and in becomes reduced, probably forming the stapes of amphibians and higher forms.

The hyoid arch proper becomes more or less intimately connected with the posterior arches, and is concerned in affording support for the tongue.

The branchial arches of the lower vertebrates are similar. In the higher vertebrates, they are reduced from behind forward, and may disappear, or give rise to laryngeal cartilages. The first arch often fuses with the hyoid.

Evolution of the Ear Ossicles

The first appearance of ear ossicles is in the Urodeles in which the stapes appears in the form of a plate, or covering over the fenestra vestibuli, and having protruding from it, the columella and extracolumella in connection with the quadrate.

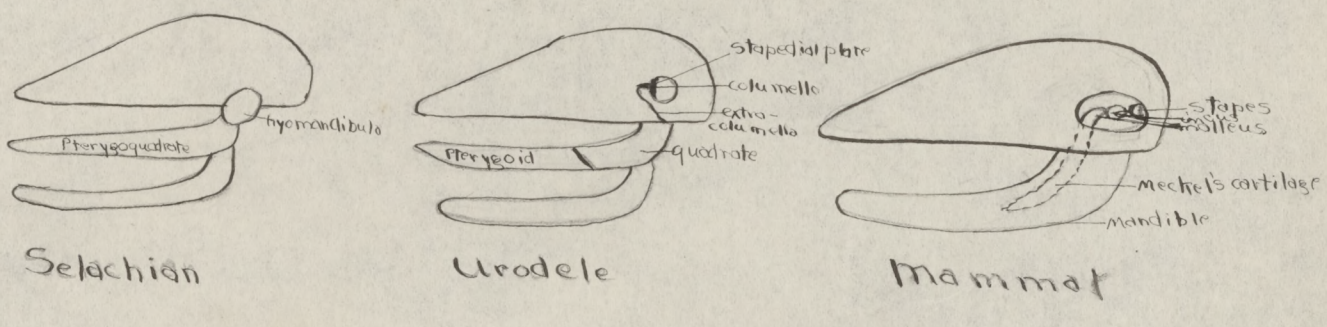
The stapes is said to be the hyomandibular arch, which has become modified. Proof of this is offered in the fact that a foramen in the hyomandibular admitting the passage of an artery seems to agree with foramen between the two sides of the stirrup in the stapes of the Sauropsida and higher mammals, thru which an artery passes.

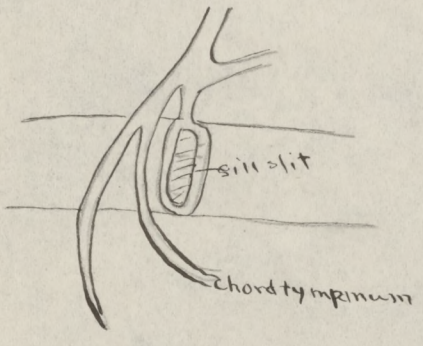
In the Amphibians and reptiles the columella is large, reaching from the tympanic membrane to the fenestra vestibuli.

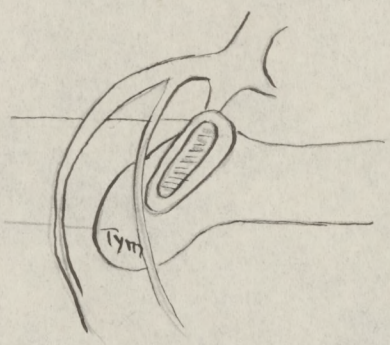
In mammals the quadrate becomes disassociated with the primitive upper jaw and migrating to the ear region becomes the incus. It is also reduced in size at this time. In a similar fashion the malleus is formed by the angulare of the mandible. At this time, the stapes becomes smaller, also, allowing room for the additional bones, which together with the stapes, form a bridge across the tympanic cavity from the tympanic membrane to the fenestra vestibuli.

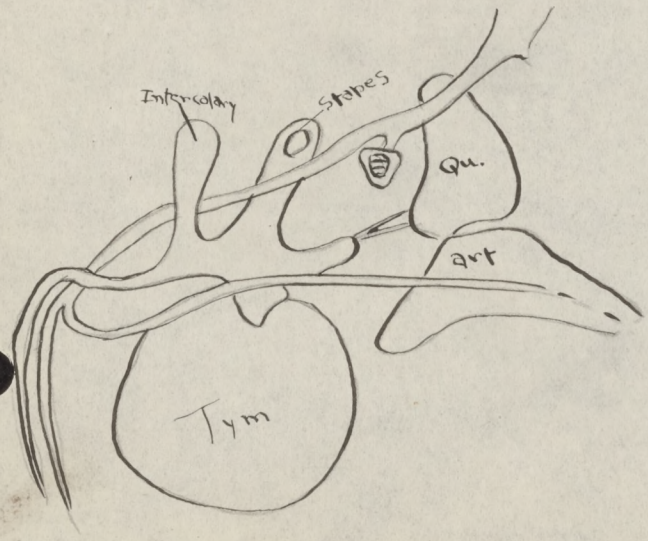
Proof of the conversion of the angulare into the malleus is afforded by the location of the auditory branch of the seventh nerve, the chorda tympani. In the embryo and in fishes this nerve goes to the first gill slit, in the later development and in amphibians and reptiles it passes into the central core of Meckel's cartilage, and in mammals it passes thru the malleus in the same way. (Plate VI)

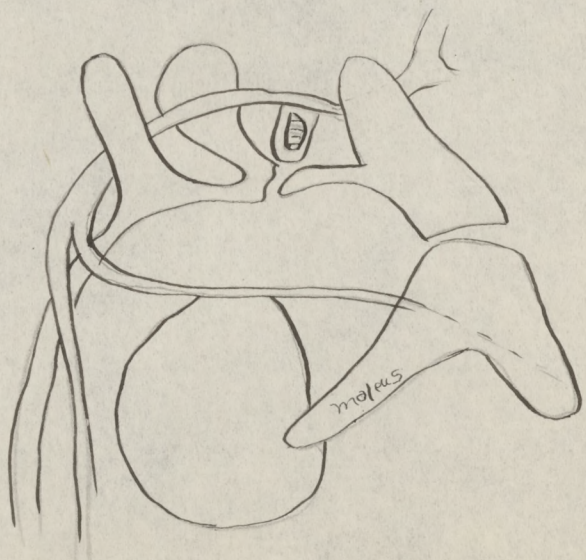
Plate VI











Appendicular Skeleton

The dermal vertical fin fold of ancestral fish was continuous around the terminus of the body. Later this became strengthened by the development of actinotrichia (slender, unjointed fin supports, arising without relation to the underlying body segments, and passing from the body wall to the margin of the fin). At this stage, motion could have been only sluggish and undulatory. With the more rapid undulation of the fin, certain points came to have greater mechanical stress and at these points, nodes arose, while at the other points, then becoming useless in motion, a gradual diminution in width occurred. This is the process by which the median fins are thought to have arisen, and it is, up to this point equally applicable to the development of the caudal fin. Firmer and stouter fin supports were produced on both the dorsal and ventral sides, but unlike the supports of the median fins, no basal elements become segmented off. The first supports occur in the region of the base of the caudal fin, for this was doubtless the region of greatest stress. Later these supports extended backward to the tip of the vertebral axis.

As cartilaginous supports originated, need for the enlargement of the ventral lobe of the caudal arose; the radials in this region became longer and stouter, and accompanying this condition is an upturning of the vertebral axis. The primitive structure of the shark's caudal fin is thought to be ancestral to the higher types of fin. That is, a heterocercal type has given rise to a homocercal type. See Plate VIII b Fig. 1, 2, 3, 4, 5

According to Wiedersheim's theory, the paired fins have also arisen from fin folds, similar in nature to the vertical fin fold, but lateral. This is in opposition to the thoery of Gegenbauer, to the effect that the origin of the paired fins has been from the hindermost gill bars.

The mode of evolution of the paired fins was doubtless similar to that described for the caudal and median fins.

At the time of the separation of the vertical fold into caudal, dorsal and anal elements, the paired fins probably arose as balancing organs, -- arising in the line of the fish's motion, and developing in the portions of mechanical stress, while the useless portions disappeared. Primitively the paired fins are represented by two pairs of keel-like lappets, the pair more anterior in position, being more important, having a greater function in balance and thus becoming more greatly modified than the posterior pair which lie in an almost motionless position. The lappet shaped fins acquire more rigid support and cartilaginous rod-like elements rise within the fin web in metameric sequence, possibly representing a fusion of actinotrichia. These are the radials, which soon segment off a proximal joint -- or basal cartilage -- not present in the caudal fin. At first the basal elements are fused into the body wall, but an articulation soon arises between the free portion of the fin and the part extending into the body-wall, and this latter part, serving as a support for the limb proper constitutes the primitive limb girdle. The arch finally extends upward to come in connection with the axial skeleton, Typically each girdle is composed of three elements, one dorsal, and two ventral.

In the pectoral girdle these elements are the scapula, and coracoid and pubis. Reinforcement of the cartilaginous elements by membrane bones occurs in the dipnoans and some ganoids, which vary thruout the higher forms. Plate VIII a

Appendicular skeleton

Homologies

Limb girdles
Limbs

Anterior limb girdle
- scapula
- clavicle
- coracoid

Ant. limb
- humerus
- radius
- ulna
- carpals
- metacarpals
- phalanges

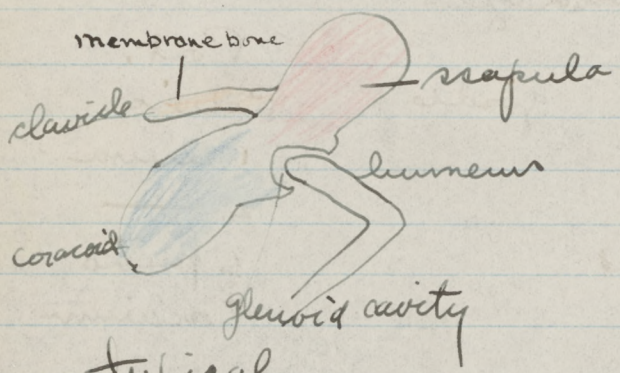
Posterior limb girdle
- ilium
- ischium
- pubis

Post. limb
- femur
- tibia
- fibula
- tarsals
- metatarsals
- phalanges

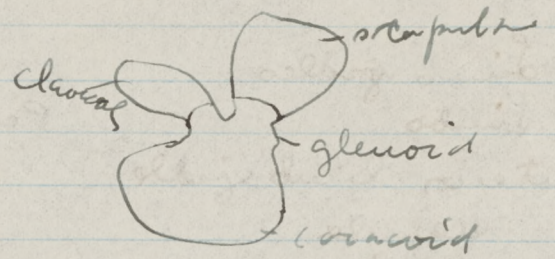
	Ant.	Post.
	Pectoral girdle	Pelvic
1.	scapula	ilium
2.	clavicle	——
3.	epicoracoid	pubis
4.	coracoid	ischium

Plate a

Urodeles



typical Fig 1.



amphibian
clavicle of frog articulates with sternum
coracoid also articulates with sternum
Anuran epicoracoid also " " "

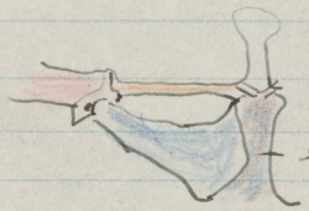


Fig. 2.

Bird

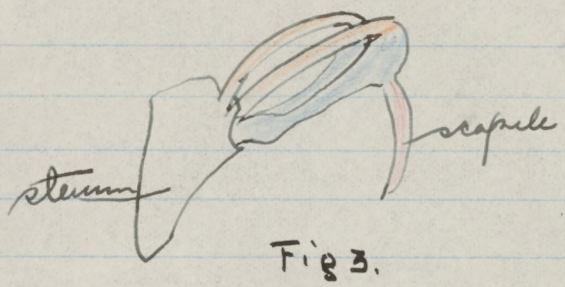


Fig 3.

glenoid cavity entirely in scapula

Monotreme

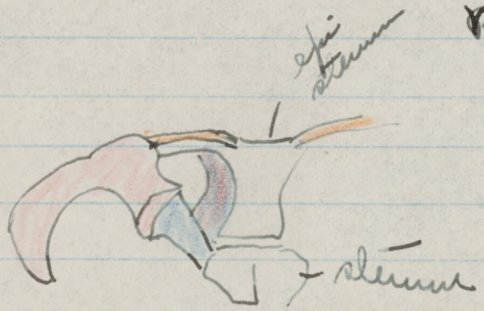


Fig. 4

epicoracoid above coracoid
not articulating with sternum
with sides of epi "

The elements of the pelvic girdle are the ilium, and ischium and pubis. The homologies with the pectoral girdle are given on Plate Its development is comparable to that of the pectoral girdle. The girdle does not become attached to the vertebral column until the tetrapods.

In the evolution of the appendages, the line of basals (following the lappet-like stage) becomes fused into a compact plate-like mass, accompanying a new motion, the animals being capable of being directed up or down, the fin becoming a direct aid in propulsion, acquiring a paddle-like function, involving also a sideways movement. With this added motion, the region of concrescence of the fin rays is transferred posteriorly and the basals and radials acquire a more jointed structure.

The radials gradually surround the distal end and the dermal region becomes increased (Plate III, Fig. 5, 6, 7, 8).

The basalia in primitive forms are large, and they support a large number of radials. Such a condition is seen in the Cladoselache (Fig. 5) The number of basalia is progressively reduced thru the higher forms, and the other parts are variously modified. In some ganoids and teleosts, the skeletal parts become ossified. The basalia shorten and become more closely associated with the girdles. The radii form most of the fin.

The fin of Ceratodus most closely approximates in function the limb type of land-living vertebrates. Gegenbaur considers this as representative, rather of the lowest type of fin from which all others have evolved. It would seem, however, that it is the highest type of fin. The suggested means of evolution of the tetrapod appendage from this fin is as follows: The persistence of a basal as a framework (humerus) of the limb, two proximal radials, as the next segment, and the skeleton of the wrist and hand from a corresponding number of distal radials on the anterior side of the fin. According to Gregory all of the dermal elements are lost in the tetrapoda.

when does the cleithrum disappear? Is not the clavicle partly a dermal element? Then some not fin elements

Plate VIIIb

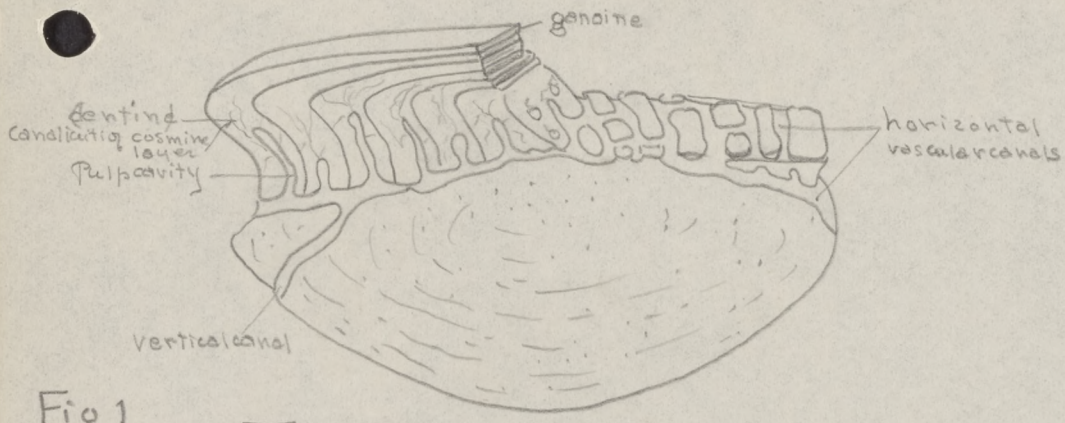
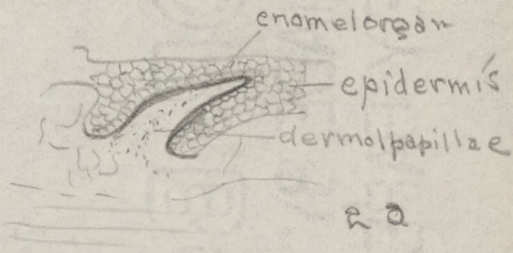


Fig 1

Tranverse section of scale of Cheirolepsis



2a

2b.

2 stages in the development of placoid scale

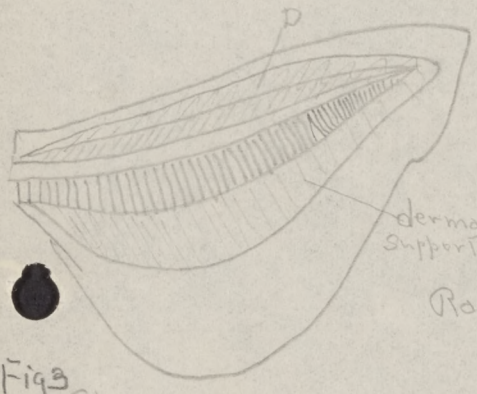


Fig 3 Shark

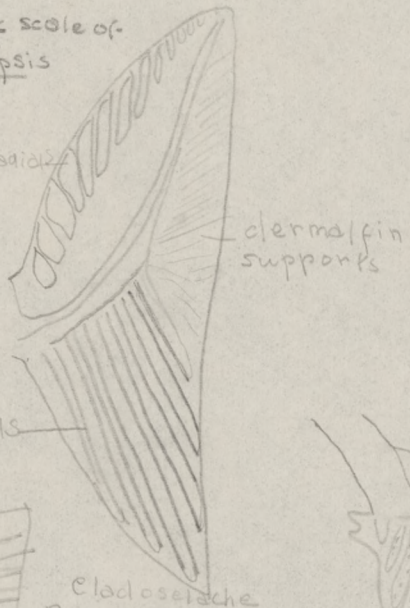
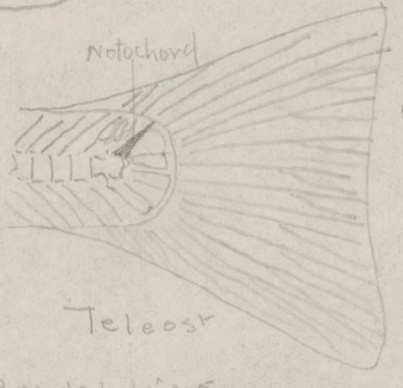


Fig 4



Figs Caudal fins

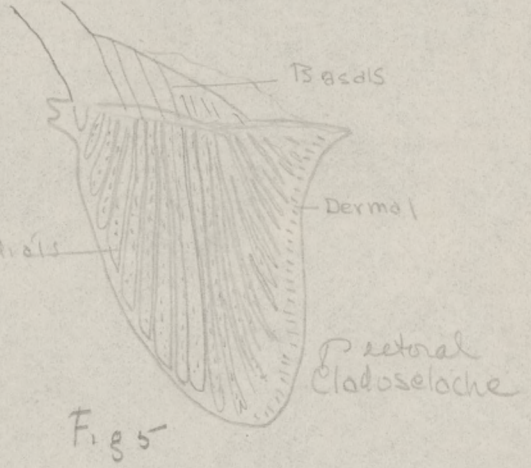


Fig 5

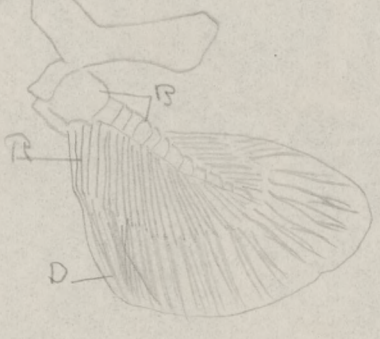


Fig 7. Xenacanthus

Fig 6. Heptanchus

Fig 8. Archipterygial fin of Ceratodus

Brain

Figures 1 to 9 of Plate XX illustrate the evolution of the brain as represented in the different animals, from the primitive state to the reptiles. A brief summary of the evolution follows.

The primary parts of the brain are: Fig. 1
- Anterior vesicle -- forebrain
- Middle vesicle -- mid-brain
- Posterior vesicle -- hind brain

All have cavities directly connected with the spinal cord.

The next step involves more parts:
- Forebrain
  - Telencephalon -- cerebral element
    - Cerebral hemispheres
    - Olfactory lobes
    - The floor forms the corpus striatum
    - The peripheral part is called the pallium
  - Diencephalon
- Mid-brain
  - Mesencephalon
    - Optic lobes dorsal -- corpora bigenina
    - Crura cerebri ventral
- Hind-brain
  - Metencephalon -- cerebellum
  - Myelencephalon

The lateral halves of the brain become connected by commissures at first very incompletely (Lamprey), later the distinction between right and left haves is well marked. The commissures are:
- Habenular commissure -- in the pallium
- Anterior commissure -- in the posterior region of the telencephalon
- Middle commissure -- in the diencephalon
- Posterior commissure -- in the anterior part of the mesencephalon
- Others in the pallial region

In the telencephalon the pallium becomes differentiated into a layer of cortical gray matter reaching its height in mammals, while in lower vertebrates the cortex is partially or entirely non-nervous, retaining the embryonic epithelial character.

The outer surface of the cerebral hemispheres is smooth except in mammals. In this group there are convolutions and fissures consisting of folds of the entire pallium or cortex.

Certain structures arise from the diencephalon
- Optic thalami -- thickenings of the basal wall
- Ganglia habernulae -- on the postero-lateral margin of the dorsal region having superior commissures between
- Optic vesicles -- paired ventro-lateral outgrowths from which the optic nerves and retina are later derived
- Pineal apparatus -- outgrowths of the roof
  - Epiphysis -- persists vestigially in all vertebrates
  - Parietal organ -- atrophies in most vertebrates
- Infundibulum -- extension of the floor with part of the hypophysis, or pituitary body. Another portion of the hypophysis is derived from the epithelium of the stomodaeum In fishes this is the saccus vasculosus.

Mesencephalon
Optic lobes subdivide in mammals into anterior and posterior lobes
Metencephalon
The cerebellum becomes folded and subdivided into medial and lateral lobes
Myelencephalon
The medulla floor becomes thickened in mammals giving rise anteriorly to a transverse band of fibers the pons Varoli.
Most cerebral nerves arise from the medulla

The walls of the vesicles thicken and their cavities form the ventricles of the brain, which undergo gradual reduction.

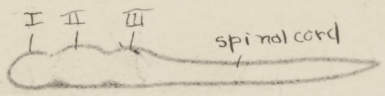
Telecoele -- anterior and paired. Gives rise later to paired cavities, the lateral ventricles. First and second ventricles
Diacoele -- third ventricle communicating with 1 and 2. Extends into the infundibulum by the foramen of Monro. May continue into the corresponding olfactory lobe, as an olfactory ventricle.
Mesocoele -- olfactory ventricle. Communicates with the opticle ventricle of the optic lobes.
Metacoele -- in the cerebellum, opening into the
Myelocoele -- fourth ventricle.

The vesicles at first lie in the same horizontal plane; later a cerebral flexure occurs and the axis of the vesicles bends down, the mesencephalon at one time forming the apex of the brain. In mammals further bending occurs, all connected with the development of the skull and the longitudinal growth of the brain.

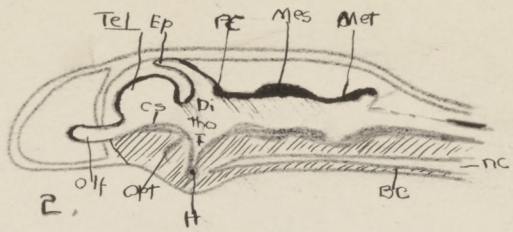
In fishes and amphibians, the cerebral flexure becomes almost obliterated, persisting, however, in mammals more markedly. In mammals the great posterior development of the cerebral hemispheres results in their overlying all other parts of the brain.

Evolution of the brain

Plate IX



1.



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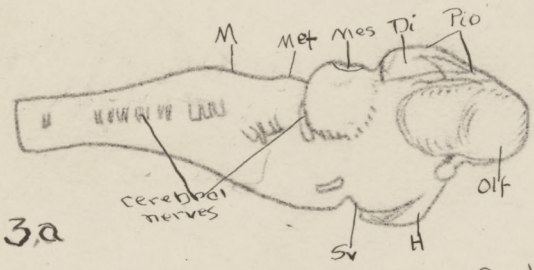
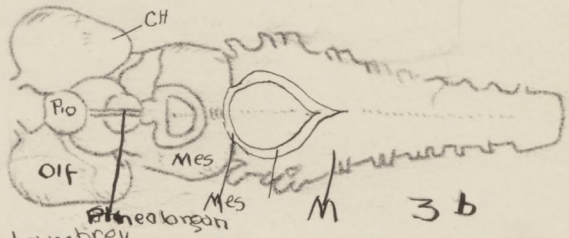
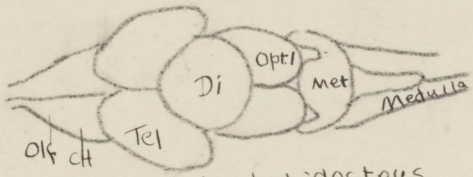


3a



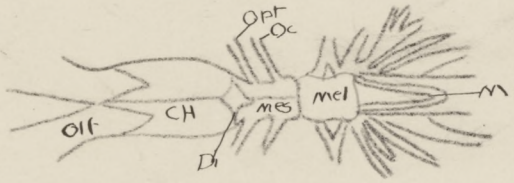
3b

Cyclostome - Lamprey

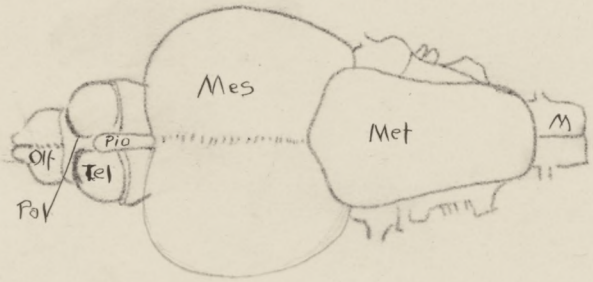


Ganoid - Lepidosteus

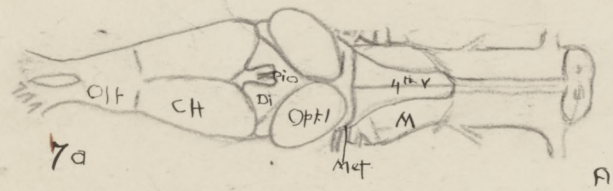
4



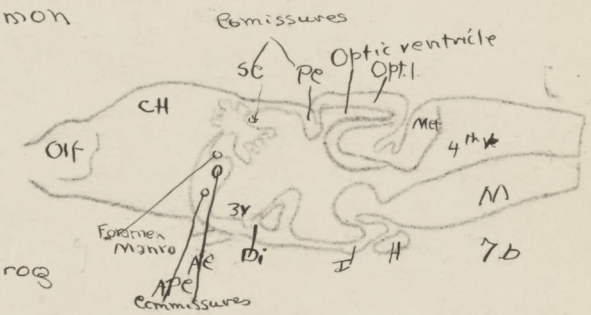
5 Dipnoi - Ceratodus



6 Teleost - Salmon

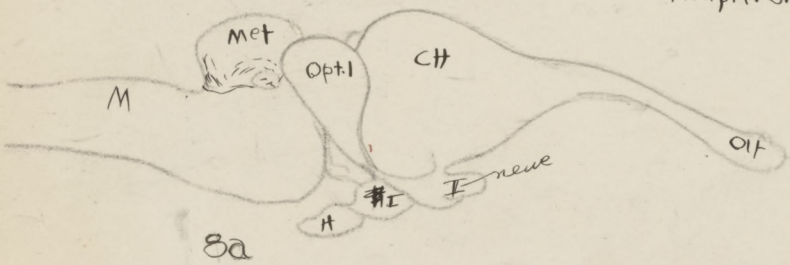


7a

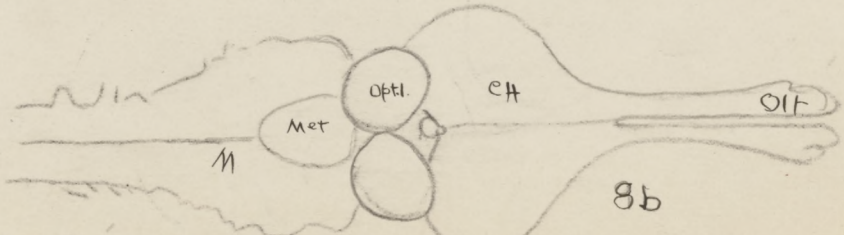


7b

Amphibian - Frog



8a



8b

Reptile - Aligator

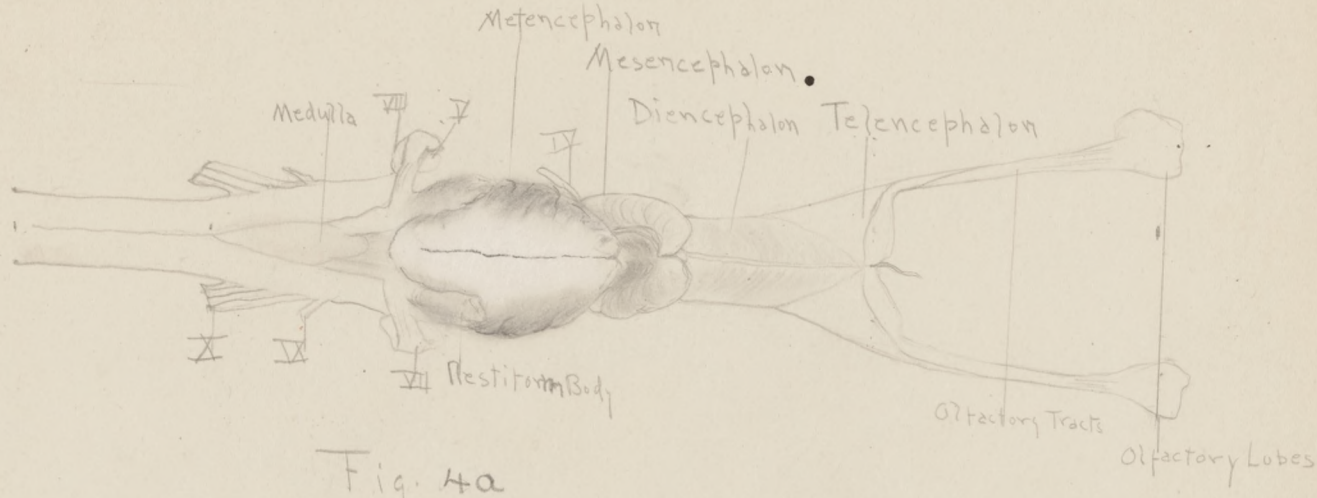


Fig. 4a
Dorsal View of Brain
of Shark

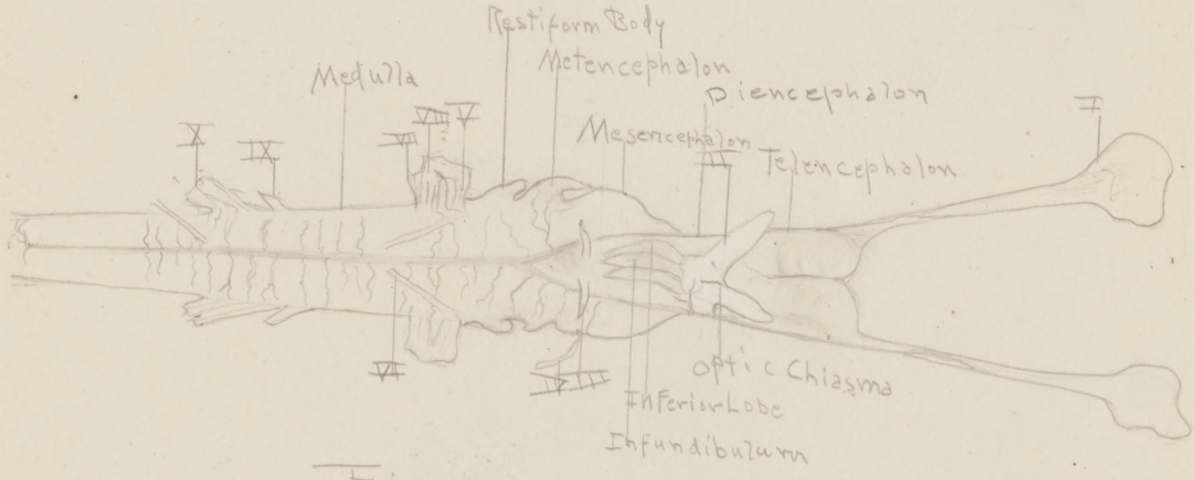


Fig. 4b
Ventral View of Brain
of Shark

Heart

The heart may be thought of as corresponding essentially to a strongly developed blood vessel, later becoming complicated by the formation of various folds and swellings.

The heart is composed of two portions
A venous portion -- the atrium into which the blood enters
An arterial portion -- the ventricle, from which the blood flows out.

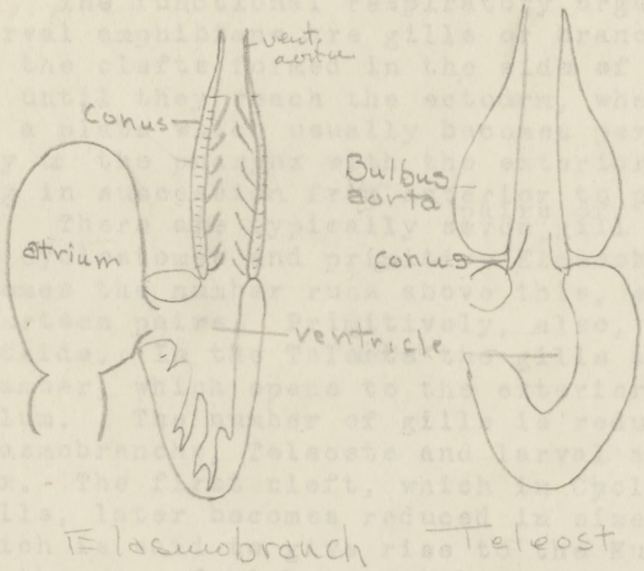
These portions become differentiated as follows:
Venous portion
Sinus venosus, opening into the atrium by a narrow aperture having two valves
Arterial portion
Truncus arteriosus
Conus arteriosus -- proximal muscular end, provided with valves
Bulbus arteriosus -- distal portion continuing forward into the ventral aorta

The ventral aorta gives off a series of afferent branchial arteries, each running between two gill-clefts and becoming continuous with the efferent branchial arteries. The first pair gives off branches to the head -- the carotids, and then they all unite above the gill clefts forming a longitudinal trunk which constitute the right and left roots of the dorsal aorta. The foregoing is the condition present in Cyclostomes, sharks and fishes, each group, having certain modifications adapted to its particular needs. The greatest change occurs with the appearance of pulmonary respiration.

Pulmonary respiration is accompanied by the formation of a septum in the atrium and in the ventricle, leading in the birds and mammals to the presence of two separate atria -- auricles, and two separate ventricles, the conus arteriosus and sinus venosus becoming eventually incorporated in the right ventricle and auricle respectively. This development is gradual, the amphibians have one ventricle and two auricles; the reptiles two auricles and an incomplete division of the ventricle.

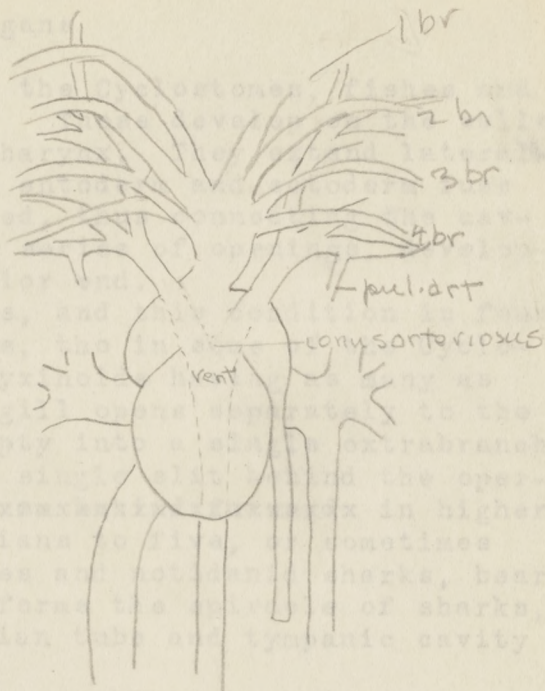
A new artery -- the pulmonary artery, arises from the last arterial arch and becomes connected with the right ventricle, carrying venous blood to the lungs. Other vessels, the pulmonary veins return the oxygenated blood from the lungs to the left auricle, thence to the left ventricle and throught the aorta into the general circulation.

Plate X

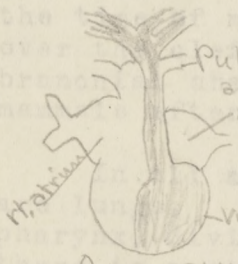


Elasmobranch

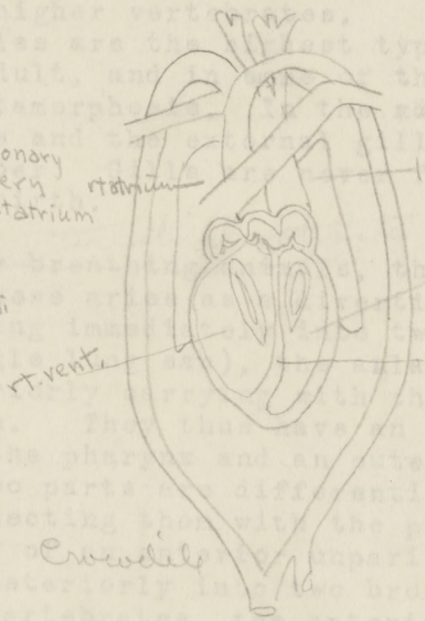
Teleost



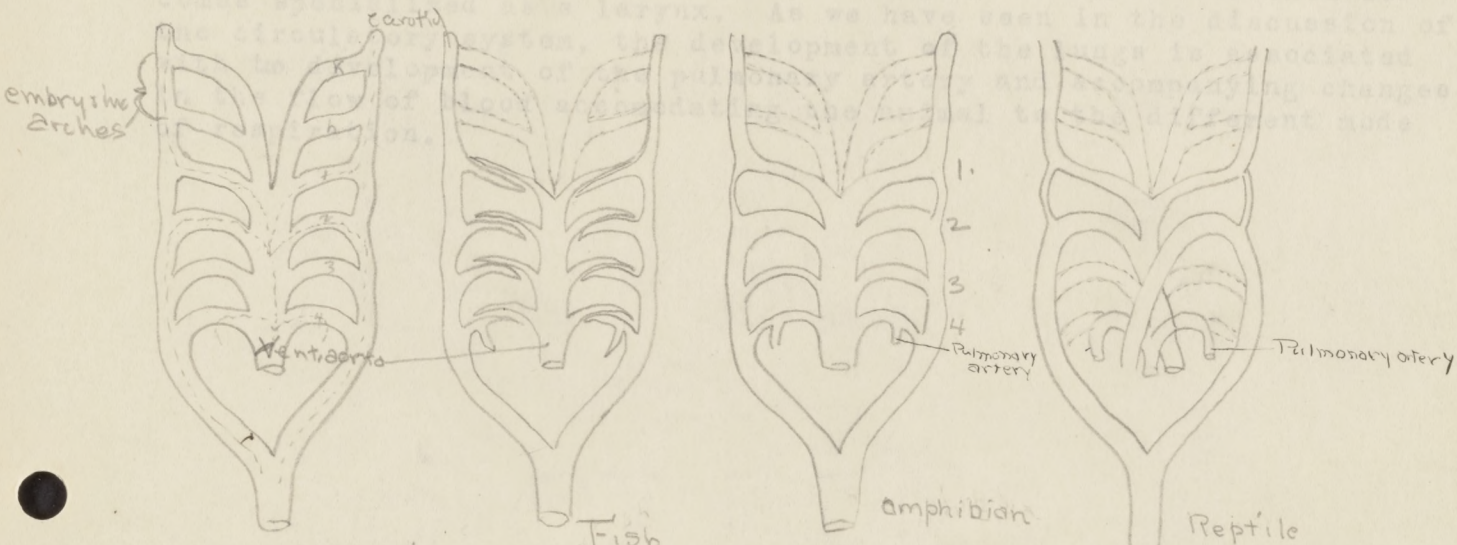
Protopterus



Anuran



Crocodile



Embryonic condition

Fish

Amphibian

Reptile

Evolution of Respiratory Organs

The functional respiratory organs of the Cyclostomes, fishes and larval amphibians are gills or branchiae. These develop on the walls of the clefts formed in the sides of the pharynx. They extend laterally until they reach the ectoderm, when the entoderm and ectoderm fuse to a plate which usually becomes perforated, thus connecting the cavity of the pharynx with the exterior by a series of openings, developing in succession from anterior to posterior end.

There are typically seven pairs of gill clefts, and this condition is found in Cyclostomes and primitive Elasmobranchs, tho in some of the Cyclostomes the number runs above this, some myxinoids having as many as fourteen pairs. Primitively, also, each gill opens separately to the outside. In the Teleosts the gills all empty into a single extrabranchial chamber, which opens to the exterior by a single slit behind the operculum. The number of gills is reduced in higher Elasmobranchs, Teleosts and larval amphibians to five, or sometimes six. The first cleft, which in Cyclostomes and notidanid sharks, bears gills, later becomes reduced in size and forms the spiracle of sharks, which is said to give rise to the Eustachian tube and tympanic cavity of the ear of higher vertebrates.

The Urodeles are the highest type of vertebrate to have functional gills in the adult, and in some of the urodeles they are absorbed at the time of metamorphosis. In the anuran the operculum grows back over the clefts and the external gills become folded into the extrabranchial chamber. Gills are never functional in either reptiles or mammals after birth.

In all ~~air breathing~~ terrestrial vertebrates animals, the functional respiratory organs are lungs. These arise as a diverticulum on the ventral side of the pharynx, dividing immediately into two sacs (In the Dipnoi, however, there is a single lung sac), the anlagen of the two lungs. The two grow posteriorly carrying with them the peritoneum and protruding into the coelom. They thus have an entodermal lining from the epithelium of the pharynx and an outer serous layer of peritoneum. At this time two parts are differentiated: the lungs themselves and air ducts, connecting them with the pharynx. The ducts themselves may be composed of an anterior unparied trachea going to the pharynx and dividing posteriorly into two bronchii which go to the lungs. In the higher vertebrates, the anterior portion of the trachea becomes specialized as a larynx. As we have seen in the discussion of the circulatory system, the development of the lungs is associated with the development of the pulmonary artery and accompanying changes in the flow of blood accomodating the animal to the different mode of respiration.

Dinosaurs.

In the Age of Reptiles - Dinosaurs were as varied as the quadrupeds of the mammals today.

The groups are as follows:

I Theropoda - carnivores

Sharp pointed teeth, sharp claw, bipedal - bird like hind feet - 3 toes (ancestrally 4) & grasping or raising fore-limbs. Head large, neck moderately long, body unarmored

A. Allosaurus, Ornithoclestes - Up. Jurassic

B Tyrannosaurus, Deinodon, Albertosaurus, Ornithomimus - Up. Cretaceous

II Sauropoda - amphibious Dinosaurs

Blunt pointed teeth, blunt claws, quadrupedal with elephant like limbs & feet. Long neck & small head. Unarmored

A Brontosaurus, Diplodocus, Camarasaurus (Morosaurus), Brachiosaurus Up. Jur. & Comanchian.

III Predentates - beaked dinosaurs

Horny beak on part of jaw, cutting or grinding teeth behind it. Herbivorous. Pelvis peculiar. Hoof instead of claws. Many genera armored.

A. Iguanodonts

Bipedal, unarmored, single row cutting teeth 3 toed hind feet. Up. Jur. Comanch & Cretaceous Camptosaurus.

B. Trachodonts - duck billed dinosaurs

like the above but with numerous rows of

small teeth set close together to form a grinding surface. Cretaceous.

Trachodon, Hadrosaurus, Claosaurus, Saurolophus
Corythosaurus.

C. Stegosaurs – Armored dinosaurs
Quadrupedal with elephantine feet, short neck, small head. Body & tail armored with massive bony plate & spines. Teeth in single row like Iguanodonts.
Stegosaurus – Up. Jurassic
Ankylosaurus – Up. Cretaceous

D. Ceratopsian or Horned dinosaurs
Quadrupeds with elephantine feet, short neck, large head with bony frill around neck – pair of horns over eyes – single horn in front. Teeth in single row, but broadened out for grinding. Usually
Triceratops, Monoclonius, Ceratops, Torosaurus, Anchiceratops. Cretaceous.

Theropoda & Sauropoda are nearly related, but the predentata form a distinct & separate group, possibly of different ancestry. The distinction is more or less based on the pelvis. That of the first two is like the majority of reptiles with pubis pointing down & forward – the ilium a high rounded plate. In the predentates it is different & strongly suggests the bird pelvis.

Dinosaurs' mall continents – chiefly Europe & N. Am.
Carnivores most wide spread – only one found in Australia
Sauropods in Europe, N. Am. India, Madagascar, Patagonia, Africa
Beaked most limited.

Carnivorous dinosaurs
1, 2 & 3

Fig. 1. Allosaurus

Fig. 2. Ornithodestes

Fig 3. Ostrich dinosaur
Struthiomimus

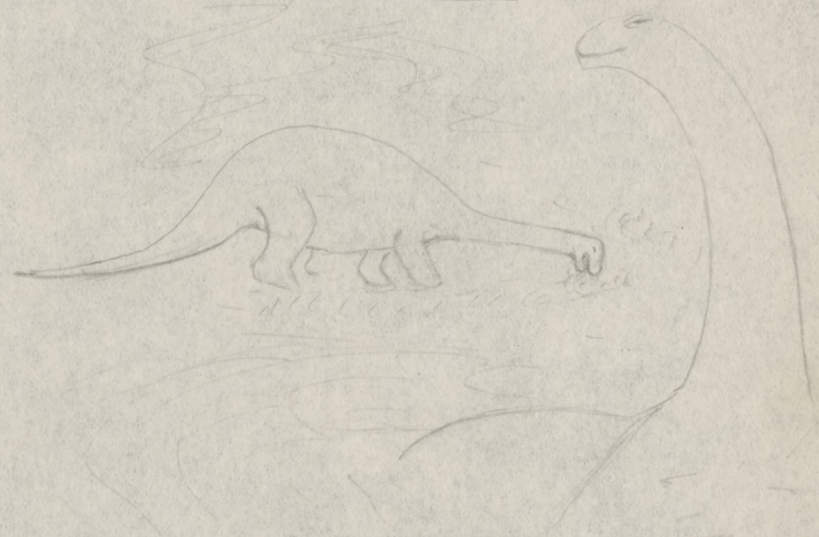


Fig. 4 Habit sketch of Sauropoda
Apatosaurus

Iguanodonts

Fig. 5. Trachodon Iguanodont

Fig. 7. Triceratops

Fig. 6. Ceratopsia

Dinosaurs

Plate XII

Anchisaurus skull Fig 1.

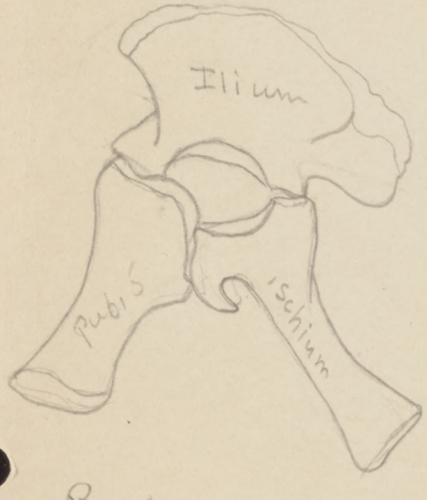
Carnivorous dinosaurs
Allosaurus

Beaked Dinosaurs
Trachodon

Amphibious Dinosaurs
Brontosaurus

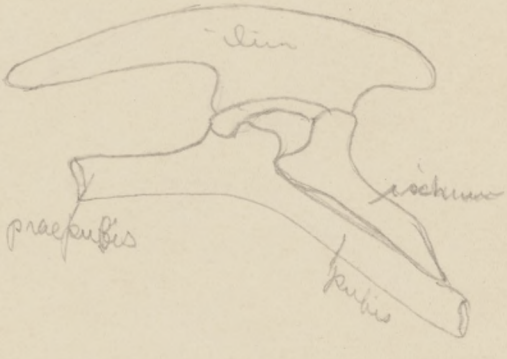
Hind feet

Saurischia



Brontosaurus

Ornithischia



Stegosaurus

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